Investigating whether structural in-stream habitat additions are an effective tool for restoring benthic communities in lowland Canterbury waterways

---

A thesis submitted in partial fulfilment of the requirements for the

Degree of Master of Science in Ecology

School of Biological Sciences

University of Canterbury

Timothy Charles Green

2018

Table of Contents

List of Figures

List of Tables

Acknowledgements

I would like to thank all of my colleagues at the School of Biological Sciences for their guidance and support, making this research possible.

I am extremely grateful for my amazing supervisory team: Jon Harding and Catherine Febria. Jon, thank you for taking me on and giving me this opportunity. Your ongoing support and knowledgeability have been fundamental in my achievements, and your fantastically dry jokes made working with you a pleasure. Catherine, not only have you gone out of you way to provide helpful feedback throughout the writing process of this thesis, but you were compassionate, encouraging, eager to help, and generally a delight to work with throughout my studies. For this I am truly thankful.

Thank you to all of my peers from the CAREX (The Canterbury Waterway Rehabilitation Experiment) and FERG (Freshwater Ecology Research Group) research groups that have helped me along the way. It has been wonderful getting to know you all, and I feel that I have made some truly great friends. I would especially like to thank Jon Harding, Angus McIntosh, Catherine Febria, Helen Warburton, Kristy Hogsden, Linda Morris, and Hayley Devlin for going the extra mile to keep these groups running smoothly and moving forward.

Thank you to Jon Harding and the IPENZ Rivers Group for funding this research, the land owners/managers that allowed me to access their waterways, and to Rosie, Clinton, Hannah, Nicky, Hayley, Alex, Katie, Issie, Kevin, Roland, and Chris for generously assisting me with field and lab work along the way.

Finally, I would like to thank my family and friends for being so incredibly encouraging and supportive throughout my studies.

Abstract

Land-use change is occurring at an unprecedented rate in New Zealand and globally. Freshwater ecosystems reflect the characteristics of their surrounding landscape, and consequentially, in-stream habitat quality is often poor. The loss of in-stream habitat is widely recognised amongst the greatest threats to benthic macroinvertebrates. However, how habitat should be most effectively restored remains a contentious topic, as landscapes are not akin, and thus the overarching effect that landscape scale processes have on the efficacy of local restoration projects is highly variable. My project aimed to identify to what extent the local restoration of structural habitats (i.e. boulders and large wood) can restore benthic macroinvertebrate communities in lowland Canterbury. I focussed on two life stages common to these fauna, benthic larvae and winged egg-laying adults. I conducted a survey of 11 forested South Island streams to determine whether benthic larvae discriminated between in-stream habitat types. This was followed by an experiment where I added cobble-boulders and large wood into three lowland Canterbury waterways with homogenous in-stream habitat to test whether these additions would improve the benthic macroinvertebrate fauna. Next, I conducted a survey of eight forested streams in Banks Peninsula, to determine whether winged adult insects preferred/avoided ovipositing on emergent cobble-boulder substrate based on microhabitat-scale physico-chemical/habitat cues. This was followed by a small-scale oviposition habitat addition experiment in a single urban waterway to test whether a more abundant and rich composition of adults would oviposit on complex surfaced substrate (i.e. rough vs. smooth surfaces). I found that microhabitat-scale benthic macroinvertebrate communities varied significantly between in-stream habitat types in forested streams. However, although cobble-boulder and wood additions

improved invertebrate abundances in lowland waterways, they did not significantly improve taxonomic richness. I also identified significant generic and family level preferences for oviposition habitat by adults in forested streams. These taxa (mostly hydrobiosids and simuliids) preferentially oviposited on larger emergent substrates in areas with high dissolved oxygen availability yet avoided substrate with less surface area availability (i.e. from embeddedness or moss cover). My small-scale oviposition habitat addition experiment was limited, as the ovipositing adult insects at my experiment site consisted of a single family-level group (Hydrobiosidae). However, I found that hydrobiosids did not oviposit in significantly higher abundances on substrate with complex surfaces. From my results, I determined that structural in-stream habitat availability may provide refugia and oviposition habitat for some taxa, but this was not the factor most limiting the restoration of benthic macroinvertebrate communities in lowland Canterbury, and should therefore not be prioritised as a restoration tool. Instead, practitioners should prioritise wider-scale factors that limit insect dispersal, such as poor landscape connectivity associated with extensive deforestation, and constrained insect oviposition due to sedimentation.

Chapter 1 - Introduction

Freshwater biodiversity in crisis

Approximately 0.01 percent of the world's water is contained in freshwater habitats, yet freshwater ecosystems are home to almost 6% of all described extant species (Dudgeon et al. 2006). Given the disproportionately high biodiversity found in these freshwater habitats, identifying the threats to freshwaters and their species, and the ways in which these may be mediated, has received much attention over recent decades.

Current estimates indicate the global human population to be in excess of 7.6 billion people, with projections estimating an increase of 1.5 billion people by 2050 (United Nations 2017). Concurrently, as the human population increases, our dependence on natural resources is ever-increasing (Foley et al. 2005). These major and often unsustainable increases in resource acquisition have had substantial effects on freshwater biodiversity worldwide (Dudgeon et al. 2006). Five key interacting factors are threatening freshwater biodiversity (Dudgeon et al. 2006). First, overexploitation directly depletes populations of target organisms. This practice is often economically incentivised and is quintessentially unsustainable (i.e. the rate of harvesting exceeds the replenishment rate of the resource). Historically this practice had targeted lower fecundity vertebrates (i.e. fish and reptiles), with little regard for the life-history and ecology of target organisms (Anthony & Downing 2001; Dudgeon et al. 2006). For example, overfishing was expected to have a principal role in the collapse of important sturgeon, salmon, and shad fish stocks in New England, USA (Lichter et al. 2006); while similar practices have been associated with the rapid decline of murray cod in Australia (Humphries & Winemiller 2009). Second,

species invasions often result in the decline of native fauna due to resource competition and predation (Ogutu-Ohwayo 1990; Townsend 2003). For example, introduced salmonids have caused widespread declines and localised extinctions of native galaxiid populations in New Zealand (Townsend 1996). This has been attributed to several factors including both competition for resources and space (McIntosh et al. 1992; Edge et al. 1993), and predation (Eldon 1979; McDowall 2006; O'Brien & Dunn 2007). Additionally, they are often tolerant to a range of environmental conditions, and have generalist feeding strategies, thus allowing them to dominate over native species in anthropogenically modified waterways (Townsend 1996; Rahel & Olden 2008). Third, flow modification resulting from the damming, storage, or extraction of water for irrigation stabilises and reduces downstream flows, truncates sediment transport, and exaggerates the effects of drought (Ward & Stanford 1995). Many of the structures used to regulate and divert flow (i.e. dams, culverts) also form barriers to the upstream migration of invertebrates and fish (Joy & Death 2001; Blakely et al. 2006). Fourth, diffuse pollutants such as nitrate, phosphorous and fine sediment can exclude intolerant taxa from local communities and alter in-stream productivity, diversity, community composition and food web dynamics (Smith 1987; Smith 2003; Burdon et al. 2013). Finally, habitat degradation is often considered the greatest threat to freshwater biodiversity (Collier 1993). It affects waterways over multiple spatial scales (Poff 1997; Lake et al. 2007), and has strong links to the abovementioned drivers of degradation (Dudgeon et al. 2006). Factors influencing habitat degradation at different scales include catchment deforestation, flow modification, channelisation (the active straightening and deepening of stream channels to facilitate catchment drainage), riparian clearing (the clearing of bankside vegetation, either actively or from grazing live stock), and active substrate removal (i.e. woody debris removal to enhance catchment drainage) (Lester & Boulton 2008).

Consequentially, waterways often have altered channel morphology, hydrology (Quinn et al. 1997), and physico-chemical in-stream conditions (Williamson et al. 1992; Quinn et al. 1997), and reduced refugia/cover and capacities to retain organic matter (Quinn et al. 1997; Negishi et al. 2002; Quinn et al. 2007). Waterways draining anthropogenically dominated catchments often have simplified in-stream communities, comprising of tolerant taxa (Harding & Winterbourn 1995; Quinn et al. 1997; Hall et al. 2001).

To date, the global status of freshwater biodiversity has not been comprehensively analysed (Dudgeon et al. 2006). However, the International Union for Conservation of Nature (IUCN) estimates that 37% of freshwater fishes in continental Europe are threatened with extinction (Freyhof & Brooks 2011). Additionally, 7%, 15%, and 28.2% of freshwater biodiversity in Southern, Central, and Northern Africa, respectively, are currently threatened, with levels of threat expected to rise due to future anthropogenic development (Darwall et al. 2009; García et al. 2010; Brooks et al. 2011). Estimates from New Zealand's Department of Conservation (DOC) suggest that 27% of fish, and 11% of invertebrates are threatened with extinction in New Zealand's freshwater habitats (Goodman et al. 2014; Grainger et al. 2014).

Historic approaches and shortcomings in freshwater restoration

In response to the global degradation of freshwater ecosystems, restoration efforts have become widespread in developed nations. In the United States alone, the projected average spending on freshwater restoration projects has exceeded one billion dollars per year since 1990 (Bernhardt et al. 2005). In a synthesis of 37,099 river restoration projects in the United Stated, Bernhardt et al. (2005) found that these projects had a range of restoration budgets, goals, and thus used different tools. Projects with lower budgets (median cost <$45,000) included excluding livestock to aid riparian recovery, creating and managing riparian buffer zones to manage water quality, adding

boulders/woody debris to improve in-stream habitat, installing fish ladders to aid fish passage, and revegetating and grading banks to improve stability (Bernhardt et al. 2005). While projects with higher median budgets (median $63,000-$812,000) included cleaning to improve aesthetics, species reintroductions, dam removal, bank and channel reshaping, constructing wetlands to manage storm water, enhancing flow regimes, reshaping banks and channels to improve floodplain connectivity, and land acquisition (Bernhardt et al. 2005). These restoration goals and tools are reflected in projects worldwide, yet limited budgets often make subsequent monitoring unfeasible, and when projects are monitored, they are rarely successful in restoring biodiversity (Bernhardt et al. 2005; Bernhardt et al. 2007; Palmer et al. 2010; Jähnig et al. 2011).

Jähnig et al. (2011) disturbingly reported that the perceived success of restoration projects by project leaders, and any successful restoration based on objective biotic metrics, were often not aligned. Project success is often a subjective matter, as many projects lack objective restoration goals, and monitoring is scarce (Bernhardt et al. 2005; Jähnig et al. 2011). Bernhardt et al. (2005) identified that higher cost projects were more likely to be monitored over those with a lower cost. Albeit, they found that only c.10% of projects had reported on monitoring or assessment. Consequentially, the vast majority of small-scale restoration projects provide little opportunity to assess the efficacy of the tools used – a costly missed opportunity as these projects cumulatively had a higher expenditure than expensive, monitored projects (Bernhardt et al. 2005).

Small-scale in-stream and bankside habitat additions are likely the most frequently used stream restoration tool (Bernhardt et al. 2005; Hilderbrand et al. 2005; McKergow et al. 2016). However, in addition to a lack of an objective framework and monitoring, they are rarely successful in improving biodiversity (Palmer et al. 2010; Nilsson et al. 2015). Nilsson et al.

(2015) reviewed 18 Finnish and Swedish restoration projects, where wood and course sediment had been used. They found that in-stream habitat complexity consistently increased in restored streams, however they found no consistent improvements to in-stream biodiversity. Similarly, Palmer et al. (2010) conducted a meta-analysis on worldwide data from 78 independent stream or river habitat restoration projects. Habitat restoration tools included the addition of artificial riffles and pools, channel reconfiguration, bed reworking, coarse substrate addition, constructed backwater eddies, woody debris addition, riparian planting, and restored braiding. They found that <3% of projects significantly increased macroinvertebrate richness at the reach scale. Following further analysis of 12 projects that tested whether natural variation in habitat heterogeneity explained patterns in invertebrate diversity, they also found that only one third reported significant relationships. Palmer et al. (2010) highlighted the context dependency of the habitat heterogeneity-biodiversity relationship in natural waterways and emphasised that the alleviation of landscape-scale degradation must be prioritised over localised habitat restoration. Notwithstanding, given the short time period allocated to monitoring most of these projects, the perceived inefficacy of local habitat restorations may alternatively, or concurrently be a symptom of insufficient time permitted for successional processes to come to fruition. For example, Harding et al. (1998) investigated how in-stream biodiversity changed between watersheds with different land-use history. They found that decades-old watershed land-use practices were the best predictor of in-stream biodiversity, while later alterations to land-use (i.e. <10-year-old riparian and watershed reforestation) were comparatively poor.

Future trajectories for stream restoration

The shortcomings of historic restoration are frequently tied to a 'field of dreams hypothesis', which assumes that the local restoration of habitat heterogeneity, without consideration of other

well documented ecological principals, will restore in-stream biota (Palmer et al. 1997; Hilderbrand et al. 2005; Lake et al. 2007). Several studies have identified historic approaches as a disconnect between ecological theory and freshwater restoration (Lake 2001; Lake et al. 2007; Parkyn & Smith 2011). This is often attributed to practitioners failing to identify and remediate the primary factors that constrain biotic recovery in restored sites. Parkyn and Smith (2011) identify these as a spatial hierarchy of constraints, firstly on dispersal, then local habitat, and finally on local biotic interactions. These constraints interact, and all are primarily influenced by landscape scale processes. Within this framework, Lake et al. (2007) described several key factors that must be considered. The primary factors limiting stream restoration are those that limit the dispersal of historic community components to restoration sites. This stems from the breakdown of landscape connectivity relative to the life-history traits of subpopulations within historic metacommunities. For example, widescale deforestation in developed areas can limit the aerial dispersal of adult aquatic insects (Petersen et al. 2004; Winterbourn et al. 2007; Didham et al. 2012), anthropogenic infrastructure such as dams and culverts can inhibit the inland movements of migratory fish and invertebrates (Joy & Death 2001; Blakely et al. 2006), and the alteration of riparian zones and in-stream physico-chemical conditions can depleate oviposition and spawning habitat (Lancaster et al. 2010; Hickford & Schiel 2014; Macqueen & Downes 2015). Alleviating these constraints may require practitioners to prioritise restoration nearby to source populations (see Huxel and Hastings (1999)), the establishment of dispersal corridors (Öckinger & Smith 2008) and fish passageways (Amtstaetter et al. 2017), and the restoration of local riparian and in-stream conditions relative to the life-history requirements of historic communities. Next, local habitat restoration must be established with regard to the food-web dynamics, and refugia requirements of historic communities. For example, allochthonous carbon

inputs (i.e. leaf litter and wood) are the primary food source for insect communities in forested streams, and thus determine food-web dynamics (Wallace et al. 1997); while refuge habitats such as large substrate, pools, and backwaters increase the resistance and resilience of in-stream communities to disturbance (i.e. spates and drought) (Nickelson et al. 1992; Matthaei et al. 1999; Matthaei et al. 2000; Magoulick & Kobza 2003; Davis et al. 2013). The interactions of in-stream biota within the local community must then be considered. Notwithstanding the limitations imposed by dispersal and local habitat, assembly rules (i.e. resource competition and predator-prey interactions) are an important consideration (Drake 1990; Belyea & Lancaster 1999). For example, introduced salmoniids deplete native fish assemblages in New Zealand, due to competition for resources and space (McIntosh et al. 1992; Edge et al. 1993), and predation (Eldon 1979; McDowall 2006; O'Brien & Dunn 2007). Thus, their exclusion is likely an important tool for stream restoration in New Zealand. Finally, successional pathways influence both the temporal aspects and the feasible endpoints of restoration. The historic failure of stream restoration to report improvements in biodiversity can often be attributed to a mismatch between the timeframes allocated to post-restoration monitoring, and the time-frames by which successional pathways operate in naturally dynamic systems. It is often assumed that succession will follow a 'rubber band' model (Sarr 2002), in which the pathway to restoration is akin to that of degradation. However, several other models have been recognised, including: 'hysteresis' or 'broken leg' (Sarr 2002), by which factors such as dispersal limitation and biotic interactions alter pathway to recovery, resulting in extended recovery times and distinct endpoints; the 'Humpty-Dumpty' model (Pimm 1991), where factors such as disturbance regimes and resource fluctuations cause a non-linear trajectory of biotic recovery, yet a stable end point; and similarly, the "shifting states" model (Lake et al. 2007), in which a lack of stability determines the recovery

path, and the endpoint, shifting (Sarr 2002). The importance of considering successional pathways has been highlighted by empirical studies, where decades-old watershed land-use practices have been the best predictor of in-stream biodiversity in restored catchments (Harding et al. 1998). Therefore, in landscapes where land-use practices have degraded both terrestrial and aquatic habitats over several centuries, expectations for localised restoration to restore biotic communities to pre-human status over years, or even decades (Harding et al. 1998), are rarely realistic.

Trends in New Zealand stream degradation, and restoration

Since human colonization in New Zealand c.750 years ago, native forest cover has declined from 82% to 24%, facilitating the development of primary industries such as agriculture and forestry, as well as industrial and urban areas (Ewers et al. 2006; Foote et al. 2015). In recent years, the dairy industry has intensified and expanded, with exports increasing in value by 460% between 1990-2012, and total land cover increasing by 46% between 1993-2012 (Statistics New Zealand 2012). Waterways draining pasture and urban dominated catchments frequently have degraded riparian margins, are channelised, and cleared of aquatic plants and wood to enhance catchment drainage (Williamson et al. 1992; Collier et al. 2009). In 1975, Hynes presented his seminal paper where he proposed "The valley rules the streams" (Hynes 1975). Since then much research has emphasised that freshwater ecosystems reflect the environmental characteristics of their surrounding landscape, a relationship that is intensified in the absence of riparian buffers in many waterways draining pasture, and also by point-source storm water inputs in urban dominated catchments (Lake et al. 2007; Collier et al. 2009; Foote et al. 2015). These waterways have higher temperatures, nutrient enrichment, suspended solids and sedimentation; and reduced shading, large woody debris (LWD) and coarse particulate organic matter (CPOM) inputs, when

compared to waterways draining forested catchments (Williamson et al. 1992; Harding & Winterbourn 1995; Quinn et al. 1997; Larned et al. 2016). Consequentially, biotic communities are frequently altered. Invertebrate communities are often simplified in impaired streams, consisting of high densities of tolerant periphyton favouring taxa, yet lower densities and fewer representatives of sensitive taxa (i.e. ephemeropterans, plecopterans, and trichopterans) (Quinn & Hickey 1990; Quinn et al. 1992; Quinn et al. 1997; Harding 2003; Collier et al. 2009). Similarly, in-stream habitat variations between forested and anthropogenically altered waterways have been associated with altered native and exotic fish densities and reduced diversity (Hanchet 1990; Jowett et al. 1996; Baillie et al. 2013; Hickford & Schiel 2014).

The management and reestablishment of riparian 'buffer' zones have been the prevailing stream restoration practice over recent decades in New Zealand (McKergow et al. 2016). This is considered best practice management for waterways draining anthropogenic catchments, as it is designed to buffer diffuse pollution inputs into waterways, increase shading and reduce water temperatures; this can reduce algal and macrophyte growth, and improve water quality for sensitive taxa (Parkyn et al. 2003; Burrell et al. 2014). Also, a useful bonus of restored riparian zones is the reestablishment of woody debris and leaf-litter inputs (McKergow et al. 2016). These structural habitats benefit in-stream biota in forested waterways by improving in-stream habitat heterogeneity (Quinn et al. 1997), and providing refugia (Parkyn & Collier 2004) and a food source for several invertebrate detritivores (Collier & Halliday 2000; Quinn et al. 2000; Collier & Smith 2003). However, the benefits of these structural habitat additions as restoration tools are currently assumed, largely based on extrapolations from relationships observed in unimpaired systems and overseas (Miller et al. 2010; McKergow et al. 2016).

In-stream communities in waterways draining anthropogenic catchments are affected by constraints across several spatial scales, unlike to those draining forested catchments. Therefore, although structural habitats can promote diverse community assemblages in forested New Zealand waterways, whether this effect is synonymous with anthropogenic waterways with simplified communities remains unclear. It is essential that restoration practices are targeted towards the complex requirements of in-stream biota across several spatio-temporal scales (Lake et al. 2007), and that informed efforts are made to alleviate constraints on recovery. Therefore, for practitioners to establish realistic goals and end-points for restoration, whether in-stream structural habitat availability is a factor currently limiting in-stream communities in impaired waterways in New Zealand therefore requires empirical investigation.

Thesis aim and structure

This thesis aims to identify the role of in-stream habitat in structuring benthic macroinvertebrate communities and test the efficacy of in-stream structural habitat additions as a restoration tool for aquatic invertebrates in channelised lowland Canterbury waterways.

Chapter One reviews international and New Zealand literature, providing global and local context regarding the issue of anthropogenically derived habitat loss in lowland waterways, the shortcomings of past restoration tools, and future trajectories of stream restoration. Chapter Two consists of a field survey across forested South Island streams to identify whether in-stream structural habitat heterogeneity plays an important role in shaping aquatic invertebrate community compositions. Additionally, this chapter documents a field experiment in channelised lowland Canterbury waterways, in which the benthic macroinvertebrate response to habitat additions was assessed. In Chapter Three I focused on characterising relationships between insect oviposition and habitat attributes. I document a field survey in forested Banks Peninsula

streams to identify the environmental cues responsible for insects preferentially ovipositing on some substrate over others. I also experimentally tested the effect of substrate surface complexity on insect oviposition in a single channelised waterway in Canterbury. The main data chapters – Two & Three – are written in manuscript-style with the intention of submission for publication. Chapter Four summarises the results of my two data chapters and draws together my findings, placing them in context of the published literature and outlines applications to/implications for New Zealand stream and river restoration.

References

Amtstaetter F, O'Connor J, Borg D, Stuart I, Moloney P 2017. Remediation of upstream passage for migrating Galaxias (Family: Galaxiidae) through a pipe culvert. Fisheries Management and Ecology 24(3): 186-192.

Anthony JL, Downing JA 2001. Exploitation trajectory of a declining fauna: a century of freshwater mussel fisheries in North America. Canadian Journal of Fisheries and Aquatic Sciences 58(10): 2071-2090.

Baillie BR, Hicks BJ, den Heuvel MR, Kimberley MO, Hogg ID 2013. The effects of wood on stream habitat and native fish assemblages in New Zealand. Ecology of Freshwater Fish 22(4): 553-566.

Belyea LR, Lancaster J 1999. Assembly rules within a contingent ecology. Oikos: 402-416.

Bernhardt ES, Palmer MA, Allan J, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J 2005. Synthesizing US river restoration efforts. Science 308(5722): 636-637.

Bernhardt ES, Sudduth EB, Palmer MA, Allan JD, Meyer JL, Alexander G, Follastad-Shah J, Hassett B, Jenkinson R, Lave R 2007. Restoring rivers one reach at a time: results from a survey of US river restoration practitioners. Restoration Ecology 15(3): 482-493.

Blakely TJ, Harding JS, Mcintosh AR, Winterbourn MJ 2006. Barriers to the recovery of aquatic insect communities in urban streams. Freshwater Biology 51(9): 1634-1645.

Brooks E, Allen DJ, Darwall W 2011. The status and distribution of freshwater biodiversity in central Africa, IUCN.

Burdon FJ, McIntosh AR, Harding JS 2013. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. Ecological Applications 23(5): 1036-1047.

Burrell TK, O'Brien JM, Graham SE, Simon KS, Harding JS, McIntosh AR 2014. Riparian shading mitigates stream eutrophication in agricultural catchments. Freshwater Science 33(1): 73-84.

Collier K 1993. Review of the status, distribution, and conservation of freshwater invertebrates in New Zealand. New Zealand journal of marine and freshwater research 27(3): 339-356.

Collier KJ, Halliday JN 2000. Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: stable habitat or trophic subsidy? Journal of the North American Benthological Society 19(1): 94-111.
Collier KJ, Smith BJ 2003. Role of wood in pumice-bed streams: II: Breakdown and colonisation. Forest Ecology and Management 177(1-3): 261-276.
Collier KJ, Aldridge BM, Hicks BJ, Kelly J, Macdonald A, Smith BJ, Tonkin J 2009. Ecological values of Hamilton urban streams (North Island, New Zealand): constraints and opportunities for restoration. New Zealand Journal of Ecology: 177-189.
Darwall W, Tweddle D, Smith K, Skelton P 2009. The status and distribution of freshwater biodiversity in southern Africa, IUCN.
Davis J, Pavlova A, Thompson R, Sunnucks P 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Global change biology 19(7): 1970-1984.
Didham RK, Blakely TJ, Ewers RM, Hitchings TR, Ward JB, Winterbourn MJ 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundamental and Applied Limnology/Archiv für Hydrobiologie 180(1): 27-40.
Drake JA 1990. The mechanics of community assembly and succession. Journal of Theoretical Biology 147(2): 213-233.
Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A-H, Soto D, Stiassny ML 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological reviews 81(2): 163-182.
Edge KA, Townsend CR, Crowl TA 1993. Investigating anti-predator behaviour in three genetically differentiated populations of non-rnigratory galaxiid fishes in a New Zealand river. New Zealand journal of marine and freshwater research 27(3): 357-363.
Eldon G 1979. Habitat and interspecific relationships of the Canterbury mudfish, Neochanna burrowsius (Salmoniformes: Galaxiidae). New Zealand journal of marine and freshwater research 13(1): 111-119.
Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK 2006. Past and future trajectories of forest loss in New Zealand. Biological Conservation 133(3): 312-325.
Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK 2005. Global consequences of land use. science 309(5734): 570-574.
Foote KJ, Joy MK, Death RG 2015. New Zealand dairy farming: milking our environment for all its worth. Environmental management 56(3): 709-720.
Freyhof J, Brooks E 2011. European red list of freshwater fishes, Publications office of the European Union Luxembourg.
García N, Cuttelod A, Malak DA 2010. The status and distribution of freshwater biodiversity in Northern Africa, IUCN.
Goodman JM, Dunn NR, Ravenscroft PJ, Allibone RM, Boubee JA, David BO, Griffiths M, Ling N, Hitchmough RA, Rolfe JR 2014. Conservation status of New Zealand freshwater fish, 2013. New Zealand Threat Classification Series 7: 12.
Grainger N, Collier KJ, Hitchmough R, Harding JS, Smith BJ, Sutherland DL 2014. Conservation status of New Zealand freshwater invertebrates, 2013, Department of Conservation.
Hall MJ, Closs GP, Riley RH 2001. Relationships between land use and stream invertebrate community structure in a South Island, New Zealand, coastal stream catchment. New Zealand Journal of Marine and Freshwater Research 35(3): 591-603.

Hanchet S 1990. Effect of land use on the distribution and abundance of native fish in tributaries of the Waikato River in the Hakarimata Range, North Island, New Zealand. New Zealand journal of marine and freshwater research 24(2): 159-171.
Harding J, Benfield E, Bolstad P, Helfman G, Jones E 1998. Stream biodiversity: the ghost of land use past. Proceedings of the national academy of sciences 95(25): 14843-14847.
Harding JS 2003. Historic deforestation and the fate of endemic invertebrate species in streams. New Zealand Journal of Marine and Freshwater Research 37(2): 333-345.
Harding JS, Winterbourn MJ 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. New Zealand journal of marine and freshwater research 29(4): 479-492.
Hickford MJ, Schiel DR 2014. Experimental rehabilitation of degraded spawning habitat of a diadromous fish, Galaxias maculatus (Jenyns, 1842) in rural and urban streams. Restoration ecology 22(3): 319-326.
Hilderbrand R, Watts A, Randle A 2005. The myths of restoration ecology. Ecology and society 10(1).
Humphries P, Winemiller KO 2009. Historical impacts on river fauna, shifting baselines, and challenges for restoration. BioScience 59(8): 673-684.
Huxel GR, Hastings A 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7(3): 309-315.
Hynes H 1975. The stream and its valley: With 4 figures and 2 tables in the text. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 19(1): 1-15.
Jähnig S, Lorenz A, Hering D, Antons C, Sundermann A, Jedicke E, Haase P 2011. River restoration success: a question of perception. Ecological Applications 21(6): 2007-2015.
Jowett IG, Richardson J, McDowall R 1996. Relative effects of in-stream habitat and land use on fish distribution and abundance in tributaries of the Grey River, New Zealand. New Zealand journal of marine and freshwater research 30(4): 463-475.
Joy MK, Death RG 2001. Control of freshwater fish and crayfish community structure in Taranaki, New Zealand: dams, diadromy or habitat structure? Freshwater Biology 46(3): 417-429.
Lake P 2001. On the maturing of restoration: linking ecological research and restoration. Ecological Management & Restoration 2(2): 110-115.
Lake P, Bond N, Reich P 2007. Linking ecological theory with stream restoration. Freshwater biology 52(4): 597-615.
Lancaster J, Downes BJ, Arnold A 2010. Environmental constraints on oviposition limit egg supply of a stream insect at multiple scales. Oecologia 163(2): 373-384.
Larned S, Snelder T, Unwin M, McBride G 2016. Water quality in New Zealand rivers: current state and trends. New Zealand Journal of Marine and Freshwater Research 50(3): 389-417.
Lester RE, Boulton AJ 2008. Rehabilitating agricultural streams in Australia with wood: a review. Environmental Management 42(2): 310-326.
Lichter J, Caron H, Pasakarnis TS, Rodgers SL, Squiers Jr TS, Todd CS 2006. The ecological collapse and partial recovery of a freshwater tidal ecosystem. Northeastern Naturalist 13(2): 153-178.

Macqueen A, Downes BJ 2015. Large-scale manipulation of oviposition substrata affects egg supply to populations of some stream-dwelling caddisflies. Freshwater Biology 60(4): 802-812.
Magoulick DD, Kobza RM 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater biology 48(7): 1186-1198.
Matthaei CD, Peacock KA, Townsend CR 1999. Patchy surface stone movement during disturbance in a New Zealand stream and its potential significance for the fauna. Limnology and Oceanography 44(4): 1091-1102.
Matthaei CD, Arbuckle CJ, Townsend CR 2000. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. Journal of the North American Benthological Society 19(1): 82-93.
McDowall R 2006. Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? Reviews in Fish Biology and Fisheries 16(3-4): 233-422.
McIntosh A, Townsend C, Crowl T 1992. Competition for space between introduced brown trout (Salmo trutta L.) and a native galaxiid (Galaxias vulgaris Stokell) in a New Zealand stream. Journal of Fish Biology 41(1): 63-81.
McKergow LA, Matheson FE, Quinn JM 2016. Riparian management: A restoration tool for New Zealand streams. Ecological Management & Restoration 17(3): 218-227.
Miller SW, Budy P, Schmidt JC 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. Restoration Ecology 18(1): 8-19.
Negishi J, Inoue M, Nunokawa M 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. Freshwater Biology 47(8): 1515-1529.
Nickelson TE, Rodgers JD, Johnson SL, Solazzi MF 1992. Seasonal changes in habitat use by juvenile coho salmon (Oncorhynchus kisutch) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49(4): 783-789.
Nilsson C, Polvi LE, Gardeström J, Hasselquist EM, Lind L, Sarneel JM 2015. Riparian and in-stream restoration of boreal streams and rivers: success or failure? Ecohydrology 8(5): 753-764.
O'Brien L, Dunn N 2007. Mudfish (Neochanna Galaxiidae) literature review, Science & Technical Pub., Department of Conservation.
Öckinger E, Smith HG 2008. Do corridors promote dispersal in grassland butterflies and other insects? Landscape Ecology 23(1): 27-40.
Ogutu-Ohwayo R 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, Oreochromis niloticus. Environmental biology of fishes 27(2): 81-96.
Palmer MA, Ambrose RF, Poff NL 1997. Ecological theory and community restoration ecology. Restoration ecology 5(4): 291-300.
Palmer MA, Menninger HL, Bernhardt E 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 55: 205-222.
Parkyn SM, Collier KJ 2004. Interaction of press and pulse disturbance on crayfish populations: flood impacts in pasture and forest streams. Hydrobiologia 527(1): 113-124.
Parkyn SM, Smith BJ 2011. Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. Environmental management 48(3): 602-614.

Parkyn SM, Davies-Colley RJ, Halliday NJ, Costley KJ, Croker GF 2003. Planted riparian buffer zones in New Zealand: do they live up to expectations? Restoration ecology 11(4): 436-447.
Petersen I, Masters Z, Hildrew A, Ormerod SJ 2004. Dispersal of adult aquatic insects in catchments of differing land use. Journal of Applied Ecology 41(5): 934-950.
Pimm SL 1991. The balance of nature?: ecological issues in the conservation of species and communities, University of Chicago Press.
Poff NL 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the north american Benthological society: 391-409.
Quinn JM, Hickey CW 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. New Zealand journal of marine and freshwater research 24(3): 411-427.
Quinn JM, Phillips NR, Parkyn SM 2007. Factors influencing retention of coarse particulate organic matter in streams. Earth Surface Processes and Landforms 32(8): 1186-1203.
Quinn JM, Williamson RB, Smith RK, Vickers ML 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 2. Benthic invertebrates. New Zealand journal of marine and freshwater research 26(2): 259-273.
Quinn JM, Smith BJ, Burrell GP, Parkyn SM 2000. Leaf litter characteristics affect colonisation by stream invertebrates and growth of Olinga feredayi (Trichoptera: Conoesucidae). New Zealand Journal of Marine and Freshwater Research 34(2): 273-287.
Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand journal of marine and freshwater research 31(5): 579-597.
Rahel FJ, Olden JD 2008. Assessing the effects of climate change on aquatic invasive species. Conservation biology 22(3): 521-533.
Sarr DA 2002. Riparian livestock exclosure research in the western United States: a critique and some recommendations. Environmental Management 30(4): 516-526.
Smith CM 1987. Sediment, phosphorus, and nitrogen in channelised surface run-off from a New Zealand pastoral catchment. New Zealand journal of marine and freshwater research 21(4): 627-639.
Smith VH 2003. Eutrophication of freshwater and coastal marine ecosystems a global problem. Environmental Science and Pollution Research 10(2): 126-139.
Townsend CR 1996. Invasion biology and ecological impacts of brown trout Salmo trutta in New Zealand. Biological Conservation 78(1): 13-22.
Townsend CR 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. Conservation Biology 17(1): 38-47.
United Nations DoEaSA, Population Division 2017. Population Facts - The impact of population momentum on future population growth. Population Facts No. 2017/4.
Wallace JB, Eggert SL, Meyer JL, Webster JR 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277(5322): 102-104.
Ward JV, Stanford J 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. River Research and Applications 11(1): 105-119.

Williamson RB, Smith RK, Quinn JM 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 1. Channel form and stability. New Zealand journal of marine and freshwater research 26(2): 241-258.
Winterbourn MJ, Chadderton WL, Entrekin SA, Tank JL, Harding JS 2007. Distribution and dispersal of adult stream insects in a heterogeneous montane environment. Fundamental and Applied Limnology/Archiv für Hydrobiologie 168(2): 127-135.

Chapter 2 - Are boulder and wood additions effective tools for restoring benthic communities in lowland Canterbury waterways?

Introduction

Since early human colonisation, New Zealand's native forest cover has decreased by three-quarters (Ewers et al. 2006). Rates of forest decline have increased 5-fold since European colonisation more than 150 years ago, resulting from a combination of primary industry (i.e. agriculture and forestry), industrial, and urban development (Ewers et al. 2006; Foote et al. 2015). In addition, New Zealand's agricultural sector has continued to expand and intensify over the last two decades (Foote et al. 2015). It has long been recognised that freshwater ecosystems strongly reflect the characteristics of their surrounding landscape (Hynes 1975). In lowland areas of New Zealand, this is enhanced by waterways being historically engineered to enhance catchment drainage. This was often done by clear-felling riparian margins, clearing in-stream macrophytes and wood, and artificially deepening and straightening channels (Williamson et al. 1992; Collier et al. 2009). Consequentially, waterways draining anthropogenic landscapes often have altered physico-chemical conditions (i.e. high fine sediments and nutrients) (McDowell et al. 2009; Burdon et al. 2013), and reduced in-stream shading and physical habitat (i.e. less flow variability, refugia/cover, and cross-boundary subsidies) (Williamson et al. 1992; Harding & Winterbourn 1995; Quinn et al. 1997; Negishi et al. 2002).

Widespread alteration and homogenisation of habitat is recognised as one of the greatest threats to aquatic invertebrates (Collier 1993; Burdon et al. 2013). For example, several studies have shown that agricultural and urban waterways have reduced richness and densities of

invertebrate taxa, fewer Ephemeropteran, Plecopteran, and Trichopteran (EPT) species, fewer pollution sensitive taxa, and higher densities of periphyton favouring taxa, compared to native forest waterways (Quinn & Hickey 1990; Harding & Winterbourn 1995; Hall et al. 2001; Collier et al. 2009). Benthic aquatic invertebrates are often primary consumers, feeding on periphyton and/or cross-boundary organic subsidies such as leaf-litter and wood (Quinn et al. 1997; Collier & Halliday 2000; Collier & Smith 2003). This makes energy and nutrients available for higher trophic levels (Mulholland et al. 1983; Grimm 1988). Considering the dominance of invertebrates in the diet of most freshwater fish in New Zealand (McDowall 1965; McDowall 1968; Sagar & Eldon 1983; Bachman 1984; McDowall 1990; Graynoth et al. 1993; Rowe et al. 2000), the availability of both invertebrate food sources and habitat is likely critical for the functioning of aquatic ecosystems in New Zealand.

Common management practices for restoring the ecological integrity of degraded lowland waterways are highly criticised as a disconnect between ecological theory and restoration practice (Lake et al. 2007; Palmer et al. 2010). Freshwater restoration projects worldwide often aim to increase in-stream habitat heterogeneity in support of the 'field of dreams hypothesis' (Palmer et al. 1997; Lake et al. 2007), which assumes that increasing in-stream habitat heterogeneity will trigger a prompt return in aquatic biodiversity. In reality, few of these projects receive pre and post-restoration monitoring (Bernhardt et al. 2005; Bernhardt et al. 2007), and when monitoring is conducted and documented, macroinvertebrates have rarely recovered (Palmer et al. 2010). Freshwater restoration in New Zealand has historically used the reestablishment and maintenance of riparian buffer zones as a standard 'best practice' tool (McKergow et al. 2016). This practice relies on excluding livestock, and then planting native vegetation at a defined zone parallel to the water's edge (usually 2-5 m in width) (Renouf &

Harding 2015). It has been shown to improve water quality by increasing shading (reducing temperature) (Davies-Colley et al. 2009; Burrell et al. 2014), and reducing diffuse pollution inputs via surface runoff (i.e. fine sediment and nutrients) (Smith 1987; Wilcock et al. 2013). Additionally, riparian buffers can improve in-stream physical habitat by reducing bank erosion and subsequent sedimentation (Williamson et al. 1992), while also providing inputs of leaf-litter and woody debris (McKergow et al. 2016). The short-term benefits of riparian zones are increasingly documented in the restoration literature (i.e. improved bank stability and reduced diffuse pollution inputs) (Parkyn et al. 2003; Greenwood et al. 2012; Collins et al. 2013; Wilcock et al. 2013). However, some studies suggest that woody riparian vegetation may take several decades or centuries to begin shedding large debris (Meleason & Hall 2005; Davies-Colley et al. 2009), and recent evidence from the Waikato region indicates that riparian planting is dominated (>80%) by non-woody species (Jones et al. 2016). Thus, potential for the benefits of woody debris additions to be empirically studied from passive riparian inputs may not be realised under monitoring time-frames. Additionally, there are no published empirical studies that document the potential for active structural habitat additions to restore benthic communities in lowland waterways in New Zealand. Expectations for woody debris inputs to improve habitat, and restore degraded aquatic communities in New Zealand waterways therefore currently rely on extrapolations from relationships documented in forested sites, or overseas studies (McKergow et al. 2016).

Evidence from forested New Zealand waterways can provide insight into how wood and other habitat attributes may offer structural improvements that beget improvements in benthic communities among restored waterways. Collier and Halliday (2000) found invertebrate communities inhabiting Pine (*Pinus radiata*) wood substrates in North Island pumice bed

streams had distinct compositions and higher densities, relative to inorganic substrates. This was attributed to wood providing both stable habitat, and a trophic subsidy for some taxa. Wood can also have compounding effects on in-stream habitat, by improving leaf-litter retention (Quinn et al. 2007), and creating pools (Parkyn et al. 2009). Furthermore, surveys have found that most invertebrate taxa prefer specific inorganic substrate sizes, and that density and richness generally increase with substrate size up to boulders (Jowett & Richardson 1990; Quinn & Hickey 1990; Jowett et al. 1991). Similarly, community compositional differences are associated with hydrological variations in water depth and velocity (Jowett & Richardson 1990; Quinn & Hickey 1990; Jowett et al. 1991).

Overseas studies have reported conflicting results regarding the efficacy of local habitat additions as a restoration tool. Lester et al. (2007) experimentally added wood to Australian agricultural waterways that had received historic 'de-snagging' (wood removal). They found that wood additions supported significantly higher invertebrate densities, taxonomic and functional diversity, and numbers of taxa sensitive to disturbance, relative to benthic and edge habitats. Similarly, a meta-analysis of 24 stream restoration projects that used wood and boulder additions, and channel reconfigurations indicated that improving in-stream habitat heterogeneity often has a positive effect on aquatic invertebrate richness (Miller et al. 2010). Although, the efficacy of treatments were not equal; for example, they found that wood additions had the strongest positive effect on invertebrate richness, followed by boulder additions, but channel reconfiguration yielded non-significant results (Miller et al. 2010). However, in a meta-analysis of 78 stream restoration projects, which used various methods to improve in-stream habitat, Palmer et al. (2010) found that only two of these projects significantly improved invertebrate

biodiversity. Both meta-analyses, however, referenced catchment conditions as the key factor determining individual project success.

Overseas research has shown equivocal results on whether local habitat addition is an effective restoration tool, yet efforts to improve biodiversity are ongoing and a priority for catchments around the world. Some failures have been attributed to the context dependency of catchment conditions (Miller et al. 2010; Palmer et al. 2010), and of the approaches used by practitioners (Miller et al. 2010). Whether local context such as attributes of lowland Canterbury waterways will support depauperate benthic communities to improve remains unclear and requires further investigation. Therefore, the objective of this study was to test whether in-stream habitat additions can be an effective tool for restoring benthic communities in lowland Canterbury drains. Specifically, my first aim was to survey several structural in-stream habitats (cobble-boulders, woody debris, leaf-packs, and gravel patches) across forested South Island streams to determine whether resident macroinvertebrate communities varied between habitat types, across several community compositional and functional metrics. This allowed me to interrogate differences in taxonomic compositions across in-stream habitat types that are common (i.e. gravel patches) and scarce (i.e. cobble-boulders, woody debris, and leaf-packs) in lowland Canterbury waterways. My second aim was then to experimentally test whether introducing two habitat types - cobble-boulders and coarse woody debris - to lowland Canterbury gravel-bed waterways that lacked in-stream habitat would significantly improve benthic macroinvertebrate community compositions, and whether results would reflect patterns identified among forested streams. I hypothesised that both types of additions would provide favourable refuge habitat, thus receive more diverse and abundant community compositions relative to gravel-bed controls; and that woody additions would provide a trophic subsidy for some in-

stream taxa, thus compositional variance would be greatest between these, and inorganic substrates.

Methods

This study comprised two approaches: a habitat use survey and in-stream habitat addition experiment. Methods undertaken are described below.

Habitat use field survey

Headwater streams draining forested catchments are minimally influenced by anthropogenic land-use practices, and therefore were assumed to have intact in-stream community compositions (Quinn et al. 1992; Quinn et al. 1997). During Autumn-Winter 2017, 11 small first-third order (i.e. headwater) forested streams were surveyed on a single occasion. Sites were located in three areas in the South Island of New Zealand, including the northern West Coast, Cass (surrounding ranges), and Banks Peninsula. Four streams were selected in each of Banks Peninsula and the West Coast, and three in Cass (Table 1). Sites within, and between regions varied substantially in altitude, geology, surrounding ecology, and associated landscape. Due to this, physico-chemical in-stream habitat conditions were not expected to be consistent between streams.

At each site, a bankside visual habitat assessment was conducted to identify the smallest viable reach length that incorporated cobble-boulders, woody debris, leaf-packs, and gravel patches. Gravel patches were treated as a control, as they best represented the bed substrate composition in lowland Canterbury waterways. Stream wetted width and in-stream physico-chemical conditions were measured at a single representative cross-section, approximately in the middle of the reach. Dissolved oxygen measurements were taken using a YSI Ecosense ODO200 meter, and temperature, pH, and specific conductivity were measured using a YSI 63 water

Table 1. Survey site locations with GPS coordinates. T1 = tributary one; T2 = tributary two; T3 = tributary three.

Region	Site	Latitude	Longitude
Banks Peninsula	Pidgeon Bay	-43.42846°	172.534693°
	Narbey (T1)	-43.483966°	173.12972°
	Narbey (T2)	-43.485185°	173.14707°
	Narbey (T3)	-43.484170°	173. 12218°
Cass	Middlebush	-43.2106°	171.455366°
	Binser	-43.01417°	171.483874°
	Peacock	-42.593448°	171.473885°
West Coast	Sandel	-41.31731°	172.13063°
	Glasseye	-41.27501°	172.05110°
	McMasters	-41.34437°	171.543444°
	Donegals	-42.425499°	171.143987°

chemistry meter. At three equidistant points along the cross section, water depth was measured, and a Flo-Mate (Model 2000) portable water current meter was used to measure mean water velocity. Shading was measured using a densiometer at three equidistant longitudinal points within the reach. Three cobble-boulders, woody debris, leaf-packs, and gravel patches were randomly selected in riffle and run habitats. Each selected cobble-boulder, woody debris, and leaf-pack was individually measured across length, width, and height to estimate habitat area. Gravel patches were defined as 30 cm^2 sections. Within each, three pebbles were randomly selected and measured (as above). Habitat sizes were defined by their respective approximate surface area. Cobble-boulder and gravel particle surface area was calculated as

1.15*(LW+LH+WH), where L, W, and H correspond to length, width, and height axes of the substrate, respectively (Graham et al. 1988). Using the same axial dimensions, woody debris, leaf-pack, and gravel patch surface area was approximated as cubic surface area 2*(LW+LH+WH). As gravel-patches were sampled in a standardised 30 cm^2 patch, height was the single source of variation in surface area. This was calculated as the mean H-axis measurement of the three reference pebbles measured from each gravel patch.

The resident benthic macroinvertebrate assemblage on each habitat type was sampled. For cobble-boulders and woody debris this was achieved by disturbing the entire submerged surface with a small brush. Dislodged macroinvertebrates were then collected with a kick-net positioned directly downstream (mesh size 500 μm). Similarly, gravel patches were disturbed by hand, and dislodged macroinvertebrates were collected in a kick-net positioned directly downstream. Leaf-packs were collected whole. All samples were immediately preserved in 70% ethanol.

Habitat addition experiment

Three comparable first to second order lowland Canterbury waterways were selected for my habitat addition experiment. Sites had similar widths, depths, flow velocities, and substrate size compositions (Table 6). All drain periurban–agriculturally dominated catchments and are typical of the lowland Canterbury region, with channels that have been historically straightened and managed for drainage, with similar silt–gravel dominated bed substrate compositions. Each site had received native riparian planting on at least one bank, at various early growth stages. Sites were located roadside to Fernside and Easterbrook Roads, Rangiora; and on a dairy farm in Leeston (Ivan's drain) (Table 2).

Table 2. Locations of habitat addition experiment sites with GPS coordinates

Site	Latitude	Longitude
Fernside Road	-43.20421°	172.354141°
Easterbrook Road	-43.21583°	172.35466°
Ivan's Drain	-43.395132°	172.223186°

Two types of habitat were selected as experiment treatments. These were river run greywacke cobble-boulders collected from the Waimakariri River, and dry and untreated Pine (*Pinus radiata*) logs. Greywacke cobble-boulders were selected as they best represent the geology of lowland Canterbury, larger inorganic substrates have had positive effects on benthic macroinvertebrate assemblages in previous studies (Quinn & Hickey 1990; Miller et al. 2010), and larger substrates are scarce in channelised Canterbury waterways (likely due to active clearing and finer sediment infilling). While similarly, the selection of *Pinus radiata* logs was due to positive benthic macroinvertebrate responses to coarse woody debris in other studies (Collier & Halliday 2000; Collier & Smith 2003; Miller et al. 2010), their availability, and the scarcity of large wood in lowland waterways (Quinn et al. 1997). Cobble-boulders were measured across three axes to estimate outer surface area, using the equation of Graham et al. (1988) (as above). Logs were measured and cut into quarters to match the average cobble-boulder surface area following the equation $SA = rh(\pi/2+2)+\pi*r^2/2$, where SA = surface area, r = quarter log radius, and h = quarter log height. My cobble-boulder substrate additions were on average 1,272 (±42 SE) cm^2 surface area, and my wood substrate closely matched these, measuring 1,318 cm^2 surface area.

During April 2017, a 33 m experimental and 33 m control reach was identified in each waterway. Control reaches were located immediately upstream from experimental reaches to

control for any confounding effects of the experimental treatments. Reach-scale physico-chemical conditions (i.e. temperature, dissolved oxygen, pH, and specific conductivity) were measured at a single representative point, using standard instruments (as above). Three equidistant cross-sections were established in each reach. At each cross section, wetted width was measured. Cross sections were divided into five equidistant points, at which depth and mean velocity measurements were taken using standard instruments (as above). Average substrate size was measured for each reach using the 'Wolman walk' method (Wolman 1954), by which 30 substrate particles were randomly measured while walking on a 'zig-zag' trajectory from the bottom to the top of each reach. In each experimental reach, 12 further cross sections were identified, evenly spaced three meters apart. Habitats were added at a random point on each cross section. Additions were arranged so conspecific habitats were not neighbouring. Cobble-boulders were placed on the bed substrate, and wood additions were orientated parallel to the flow and inconspicuously fastened to the bed with warratahs.

Habitat additions were sampled for benthic invertebrates on a single occasion in August 2017. The submerged surfaces of habitat additions were disturbed with a small brush, and dislodged macroinvertebrates were collected in a kick-net (mesh size 500 µm) positioned directly downstream. Six bed substrate (control) samples were then taken at laterally random equidistant points along each upstream control reach. Sample patch size was visually determined to match the average bed patch size covered by each habitat addition. Bed substrate was disturbed by hand and dislodged macroinvertebrates were collected in a kick-net positioned directly downstream (mesh size 500 µm). All samples were immediately preserved in a 70% ethanol solution.

Laboratory methods

The abundances of benthic macroinvertebrates across samples were highly variable. Samples were randomly split into eighths and sub-samples were then passed through a 500 μm sieve. Macroinvertebrates were counted and identified using a binocular stereoscopic microscope, to the lowest taxonomic level feasible following Winterbourn et al. (1989). Briefly, megalopterans, mecopterans, and neuropterans were identified to species level. Ephemeropterans, plecopterans, trichopterans, dipterans (excluding Chironomidae), and gastropods were identified to genus level. Chironomids were identified to subfamily level, other arthropods and oligochaetes were identified to sub-class level, odonates were identified to order level, and Platyhelminthes were identified to phylum level. Taxa were assigned to functional feeding groups (collector-browser, filter-feeder, shredder, and predator) following the descriptions of Cowie (1980), and the online insect identification guides provided by Landcare Research (Manaaki Whenua - Landcare Research 2018). If <200 invertebrates were found in a sub-sample, the subsample size would increase (i.e. from one eighth, to one quarter, and so on), until either >200 invertebrates were counted, or the full sample was processed. The remaining (unprocessed) sub-sample portion was then visually scanned, and any taxa new to the respective sample were identified and counted. Macroinvertebrate counts were then scaled relative to the portion sampled, excepting those counted during the visual scan.

Data analysis

All data analysis was conducted using the open-source statistical data analysis software, R (R Core Team, 2013). Several parameters were calculated to describe the benthic macroinvertebrate community composition on habitats. These included measures of total abundance; total richness;

Shannon-Wiener diversity; EPT (Ephemeroptera, Plecoptera, and Trichoptera), mollusc, and dipteran abundances and richness; and functional feeding group abundances and richness. The Shannon-Wiener diversity index is calculated as $H'=\sum pi \ln pi$, where pi is the portion of individuals found in species i. This index differs from richness calculations as it further incorporates the relative abundance of taxa, and thus evenness of the community composition (Hill 1973).

For the field survey, the effect of substrate size on benthic macroinvertebrate abundance was tested using a negative binomial mixed effects model, from the glmmADMB package in R (Fournier et al. 2012). This model family was selected as the data set had greater variability than what was predicted from a Poisson model (overdispersion), the more conventional method for analysing count data. It follows the same mean structure as a Poisson regression, however adds an extra parameter to model overdispersion. Stepwise AIC (Akaike information criterion) model selection was used to define the components retained as random effects in all models (Symonds & Moussalli 2011). For this model, habitat type, and sites nested within region were defined as random effects; while size was defined as a fixed effect. Similarly, the effect of habitat size on total richness was tested using a Poisson mixed effects regression model, and a linear mixed effects regression model was used to test this effect on Shannon-Wiener diversity, with the same fixed and random effects structure.

Negative binomial mixed effects regression models were used to test the effect of habitat type on total macroinvertebrate abundance, EPT, mollusc, and dipteran abundances, and functional feeding group abundances in survey streams, using the glmmADMB package in R (Fournier et al. 2012). The effect of habitat size on benthic macroinvertebrate abundance was preestablished, and macroinvertebrate counts were transformed into densities by offsetting

abundances by habitat size. Habitat type was defined as a fixed factor, while study site was defined as a random factor. Shredders were rare and had several zero-counts; thus, a zero-inflated model was used for this group. This method models zero-counts separately, under the assumption that some zero-counts are generated by a separate process to non-zero values. This was justified in this case by the rarity of this group at Pidgeon Bay and Narbey (T1) Streams.

Poisson mixed effects models were used to test the effect of habitat type on taxonomic richness for EPT taxa, dipterans, molluscs, functional feeding groups, and combined taxa in survey streams, using the lme4 package in R (Bates et al. 2014). As above, habitat type was defined as a fixed effect in these models, while study site was retained as a random effect following AIC selection. A zero-inflated model was used to model shredder richness. Shannon-Wiener diversity was calculated for the total species assemblage on each habitat. A linear mixed effects regression model was used to test the effect of habitat type on this metric, following the same fixed and random effects structure as above, using the lme4 package in R (Bates et al. 2014).

For the habitat addition experiment, negative binomial mixed effects models were used to test the effect of habitat type on total benthic macroinvertebrate abundance, EPT, mollusc and dipteran abundances, functional feeding group abundance, and EPT richness, using the glmmADMB package in R (Fournier et al. 2012). In these models, habitat type was defined as a fixed factor, while experiment site was defined as a random factor to control for site-scale variability. Total richness, mollusc and dipteran richness, and functional feeding group richness were analysed using Poisson mixed effects regression models. As above, habitat type was defined as a fixed factor, while experiment site was defined as a random factor. Shannon-Wiener diversity was calculated for the total species assemblage on each of the habitat additions, and

controls. A linear mixed effects regression model was used to test the effect of habitat type on this metric, following the same fixed and random effects structure as above, using the lme4 package in R (Bates et al. 2014).

Tukey's HSD post-hoc tests were used to test the significance and extent of pairwise mean differences in macroinvertebrate community metrics between habitat types in survey streams, and between habitat additions and controls at experiment sites.

Community composition differences between habitat types in survey streams, and habitat additions and controls at experiment sites, were analysed using analysis of similarity (ANOSIM), from the *vegan* package in R (Oksanen et al. 2011). This analysis was conducted on Bray Curtis distance matrices of the dataset subset by pairs of habitat types. The statistic returned is based on the difference of mean ranks between groups (habitat types) relative to differences within groups. The significance of the test statistic was based on 999 permutations of the grouping vector (constrained within survey/experiment sites), which provided empirical distributions of test statistic under a null model. When multiple pairwise comparisons are made, such as in this case, the likelihood of a type 1 error is inflated. To counteract this, the Bonferroni correction (α/n, where n is the number of tests conducted) was used, adjusting the alpha level relative to the number of pairwise comparisons made (Armstrong 2014).

Results

Habitat use field survey

Physico-chemical conditions were highly variable amongst survey streams. However, all streams had cobble dominated beds with occasional or frequent larger boulders, and dissolved oxygen concentrations were consistently high (Table 3).

Table 3. Reach-scale physico-chemical conditions amongst survey sites. Temp. = temperature; DO = dissolved oxygen; Cond. = specific conductivity; Vel. = water velocity; T1 = tributary one; T2 = tributary two; T3 = tributary three

Site	Mean shade (%)	Temp. (°C)	DO (mg L^{-1})	pH	Cond. (μS_{25} cm^{-1})	Mean wetted width (m)	Mean depth (m)	Mean vel. (m s^{-1})
Pidgeon Bay Stream	85	10.9	11.1	7.4	165	3.6	0.36	0.16
Narbey (T1)	84	6.8	11.7	6.7	87	2.5	0.13	0.09
Narbey (T2)	87	8.3	11.6	7.6	105	2.3	0.13	0.20
Narbey (T3)	92	7.0	11.7	8.4	70	2.1	0.09	0.09
Sandel Creek	92	8.0	11.4	8.2	81	0.7	0.05	0.29
Glasseye Creek	30	8.8	11.4	7.8	105	2.1	0.15	0.53
McMaster's Creek	85	9.1	11.7	7.2	118	1.2	0.09	0.15
Donegal's Creek	88	4.8	13.0	6.4	18	4.1	0.12	0.12
Middlebush Stream	86	4.9	12.1	7.6	73	1.1	0.09	0.22
Binser Stream	69	4.4	12.2	7.9	51	3.7	0.08	0.35
Peacock Stream	79	4.5	12.1	6.3	55	2.2	0.06	1.24

The mean surface area within and between habitat types surveyed was highly variable. Cobble-boulders measured on average 1876 (±106 SE) cm^2, woody debris 2683 (±343 SE) cm^2, leaf-packs 1116 (±131 SE) cm^2, and gravel patches 2101 (±2 SE) cm^2. The mean pebble size in gravel patches was 68 (±8 SE) cm^2. Habitat size had a significant positive effect on benthic macroinvertebrate abundance ($b = 0.0003$, $SE = 0.00006$, $z = 5.05$, $p < 0.001$), but did not affect other community metrics ($p > 0.05$).

A total of 95 taxa were identified across all habitats. Cumulative taxonomic richness was highest on leaf-packs (85), followed by woody debris (75), cobble-boulders (72), and gravel patches (67). This was reflected in richness values, where leaf-packs had the highest mean taxonomic richness (22.1 ± 0.96 SE), followed by woody debris (20.88 ± 1.1 SE), cobble-

boulders (19.9 ± 1.04 SE), and gravel patches (15.30 ± 0.96 SE) (Figure 1A). Mean densities followed the same trend, as leaf packs had on average 10,513 (±2822 SE) individuals per m^2, woody debris 1,554 (±361 SE) per m^2, cobble-boulders 1,317 (±195 SE) per m^2, and gravel patches (controls) 646 (±90 SE) per m^2 (Figure 1B). However, Shannon-Wiener diversity values indicated that leaf-pack communities were distinctly uneven, as mean diversity scores were highest for cobble-boulders (2.21 ± 0.08 SE), and woody debris (2.19 ± 0.06 SE), followed by leaf-packs (1.95 ± 0.08), and gravel patches (1.88 ± 0.09 SE) (Figure 1C). Habitat type explained little variation in community assemblages from presence/absence data (Figure 2A), however communities were more distinct when relative densities were included (Figure 2B). Hard substrate (i.e. cobble-boulders and gravel patches) appeared to have similar densities and taxa, while organic substrate (i.e. leaf-packs and wood) appeared to differ from others. ANOSIM indicated that community composition varied significantly between all habitats. This variation was greatest between leaf-packs and gravel patches ($R = 0.69$, $p < 0.01$), followed by leaf-packs and cobble-boulders ($R = 0.45$, $p < 0.01$), leaf-packs and woody debris ($R = 0.34$, $p < 0.01$), woody debris and gravel patches ($R = 0.20$, $p < 0.01$), cobble-boulders and gravel patches ($R = 0.11$, $p < 0.01$), and cobble-boulders and woody debris ($R = 0.04$, $p < 0.01$).

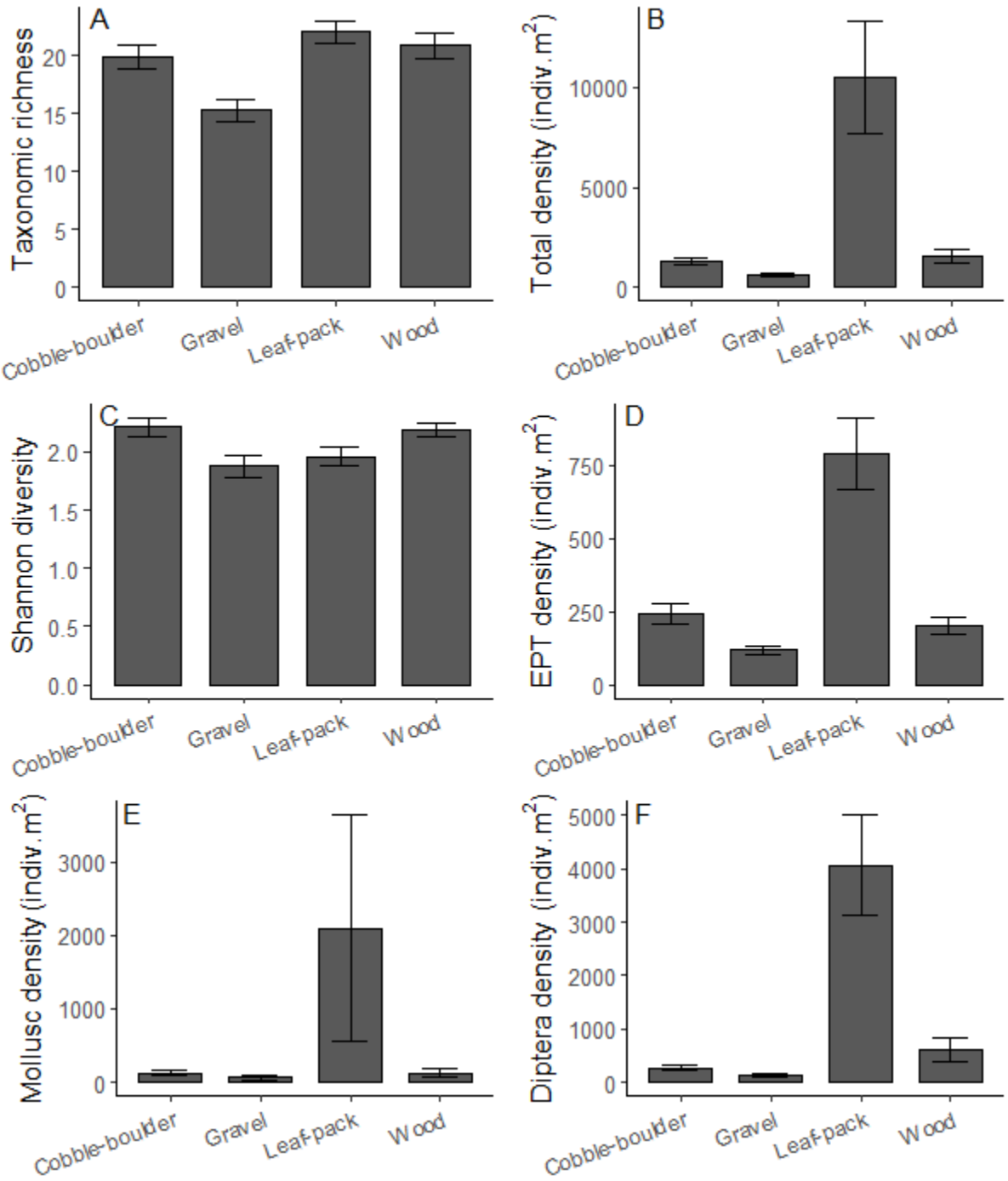

Figure 1. Macroinvertebrate distribution ($\bar{x}$ ± SE) across several community compositional metrics, amongst in-stream habitat types (i.e. cobble-boulders, gravel patches, leaf-packs, and woody debris) surveyed in 11 forested South Island streams. A, taxonomic richness; B, total macroinvertebrate densities; C, Shannon-Wiener diversity; D, pooled EPT (Ephemeroptera, Plecoptera, and Trichoptera) densities; E, mollusc densities; and F, dipteran densities.

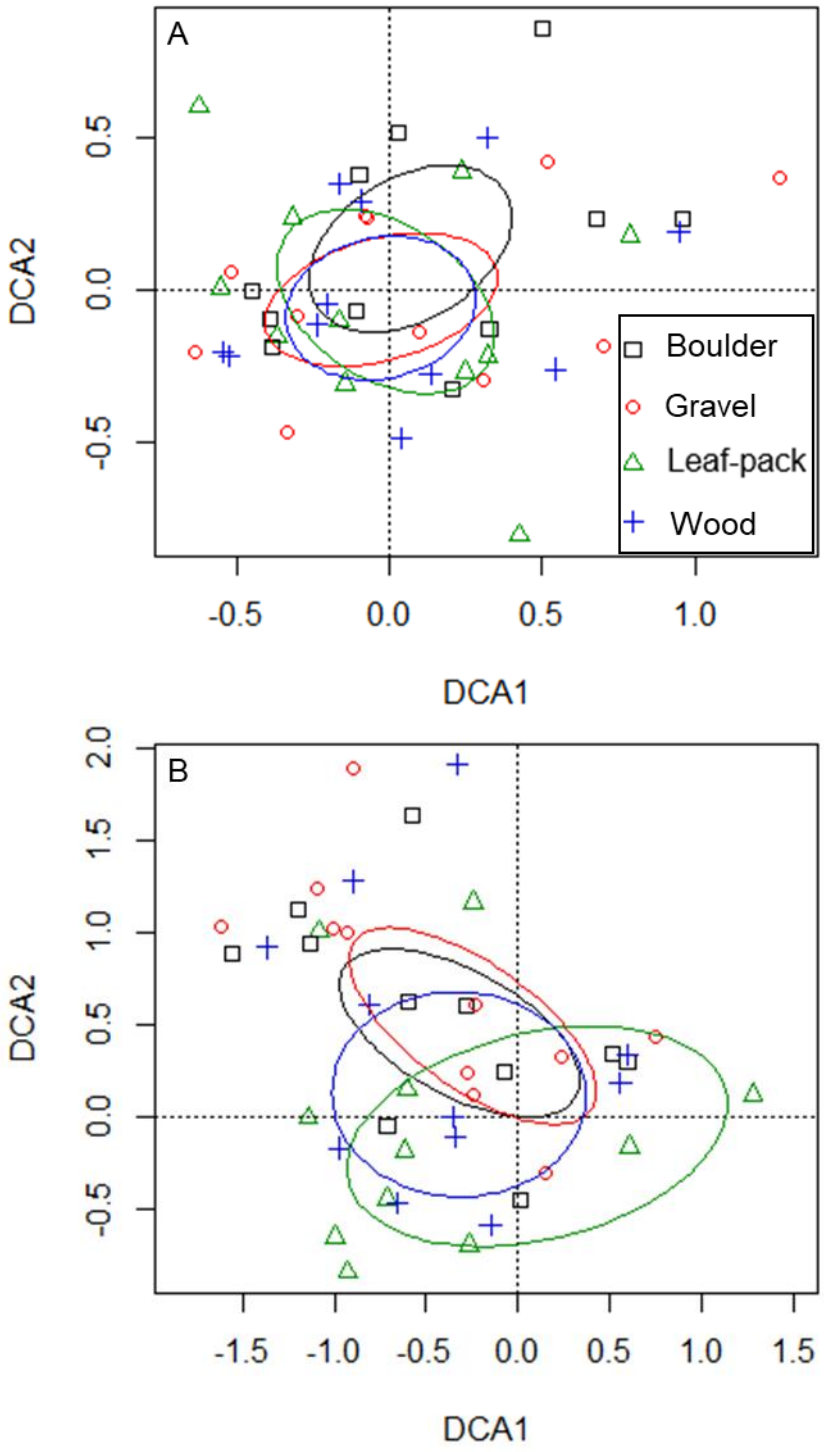

Figure 2. Unconstrained ordination (detrended correspondence analysis) biplot of community compositions amongst habitat types (i.e. cobble-boulders, gravel patches, leaf-packs, and woody debris) surveyed in 11 forested South Island streams. A, presence/absence community data; and B, community density data.

Tukey's HSD post-hoc tests showed that gravel patches had significantly lower mean taxonomic richness than all other habitats (leaf-pack – gravel patch ($b = 0.37$, $SE = 0.08$, $z = 4.61$, $p < 0.001$); woody debris – gravel patch ($b = 0.31$, $SE = 0.08$, $z = 3.88$, $p < 0.001$); gravel patch – cobble-boulder ($b = -0.26$, $SE = 0.06$, $z = -4.45$, $p < 0.001$)), but richness did not significantly vary between cobble-boulders, woody debris, and leaf-packs ($p > 0.05$). Similarly, gravel patches had significantly the lowest mean macroinvertebrate densities (leaf-packs – gravel-patches ($b = 2.64$, $SE = 0.24$, $z = 11.03$, $p < 0.001$); gravel patch – cobble-boulder ($b = -0.76$, $SE = 0.17$, $z = -4.52$, $p < 0.001$); woody debris – gravel patch ($b = 0.73$, $SE = 0.24$, $z = 3.03$, $p < 0.05$)), while leaf-packs had significantly higher mean densities than all other habitat types (leaf-packs – cobble-boulders ($b = 1.88$, $SE = 0.17$, $z = 11.04$, $p < 0.001$); woody debris – leaf-packs ($b = -1.91$, $SE = 0.24$, $z = -8.03$, $p < 0.001$)). Mean macroinvertebrate densities on cobble-boulders and woody debris did not significantly differ ($p > 0.05$). Cobble-boulders had significantly higher mean Shannon-Wiener diversity values than leaf-packs (leaf-pack –cobble-boulder ($b = -0.26$, $SE = 0.09$, $z = -2.81$, $p < 0.05$)) and gravel patches (gravel patch – cobble-boulder ($b = -0.33$, $SE = 0.09$, $z = -3.68$, $p < 0.01$)); while woody debris had significantly higher values than gravel patches (woody debris – gravel patches ($b = 0.31$, $SE = 0.09$, $z = 3.42$, $p < 0.01$)).

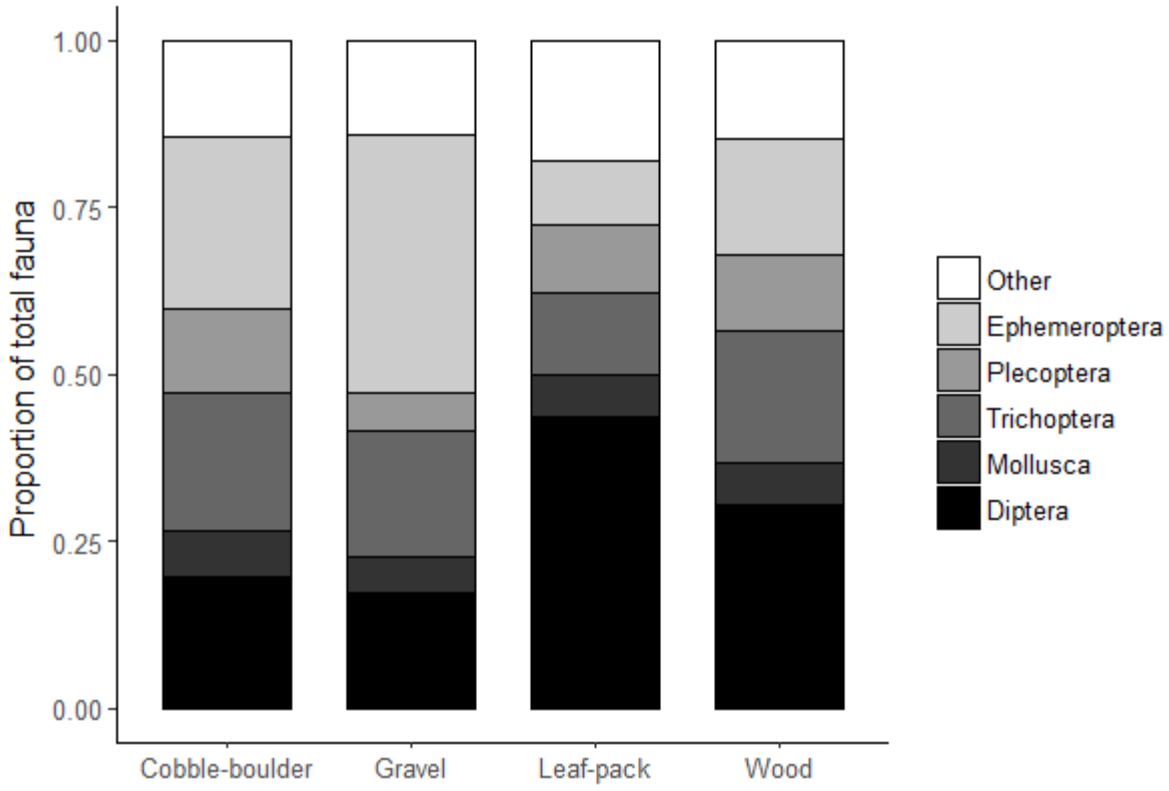

Figure 3. Proportions of common order-level macroinvertebrate groups sampled on cobble-boulder, gravel, leaf-pack, and wood habitats in 11 forested South Island streams.

Although proportions of different orders and taxonomic groups differed between habitat types (Figure 3), high variability in relative densities overwhelmed these patterns in pairwise statistical analysis (Figure 1D-F). EPT taxa were proportionately poorly represented on leaf-packs (Figure 3), however leaf-packs had significantly higher densities of these taxa when compared all other habitats (Table 4). Conversely, gravel patches which were proportionately dominated by EPT taxa, had significantly lower densities than all except woody debris, which did not significantly differ from either inorganic substrates (Table 4). EPT richness varied little amongst habitat types; however, pairwise comparisons indicated that cobble-boulders supported a richer EPT fauna when compared to gravel patches (gravel patches – cobble-boulders ($b = -2.36$, $SE = 0.08$, $z = -2.78$, $p < 0.05$)).

Table 4. Tukey's HSD post-hoc mean comparisons of common macroinvertebrate order densities (EPT = pooled Ephemeroptera, Plecoptera, and Trichoptera) between in-stream habitats surveyed in 11 forested South Island streams. * = significant; ** = very significant; *** = highly significant.

Taxa group	Habitat (I)	Habitat (J)	Mean difference (I-J)	Std. error	z	p
EPT						
	Leaf	Gravel	1.827	0.269	6.798	**<0.001*** **
	Leaf	≥ Cobble	1.141	0.192	5.951	**<0.001*** **
	Wood	Leaf	-1.436	0.269	-5.346	**<0.001*** **
	Gravel	≥ Cobble	-0.685	0.187	-3.669	**<0.01** **
	Wood	Gravel	0.390	0.268	1.457	0.438
	Wood	≥ Cobble	-0.295	0.189	-1.563	0.376
Mollusca						
	Leaf	Gravel	2.744	0.576	4.763	**<0.001*** **
	Wood	Leaf	-1.877	0.533	-3.520	**<0.01 ** **
	Gravel	≥ Cobble	-1.451	0.416	-3.489	**<0.01** **
	Leaf	≥ Cobble	1.292	0.408	3.169	**<0.01** **
	Wood	Gravel	0.867	0.548	1.582	0.370
	Wood	≥ Cobble	-0.585	0.378	1.546	0.391
Diptera						
	Leaf	Gravel	3.613	0.220	16.455	**<0.001*** **
	Leaf	≥ Cobble	2.596	0.216	12.046	**<0.001*** **
	Wood	Leaf	-2.088	0.212	-9.831	**<0.001*** **
	Wood	Gravel	1.525	0.221	6.889	**<0.001*** **
	Gravel	≥ Cobble	-1.017	0.220	-4.628	**<0.001*** **
	Wood	≥ Cobble	0.509	0.219	2.324	0.092

Similar relationships were found for molluscan and dipteran taxa. Gravel patches had significantly lower densities of molluscs and dipterans compared to other habitats, although mollusc densities were not significantly different from woody debris (Table 4). Leaf-packs had significantly higher densities of these taxa compared to all other habitats (Table 4). Again, woody debris and cobble-boulders did not significantly differ (Table 4). Mollusc richness did not significantly vary between habitat types; however, mean dipteran richness was significantly higher on leaf-packs and woody debris, relative to gravel patches (leaf-packs – gravel patches (b

= 0.47, SE = 0.16, z = 2.88, p <0.05); woody debris – gravel patches (b = 0.46, SE = 0.16, z = 2.82, p <0.05)).

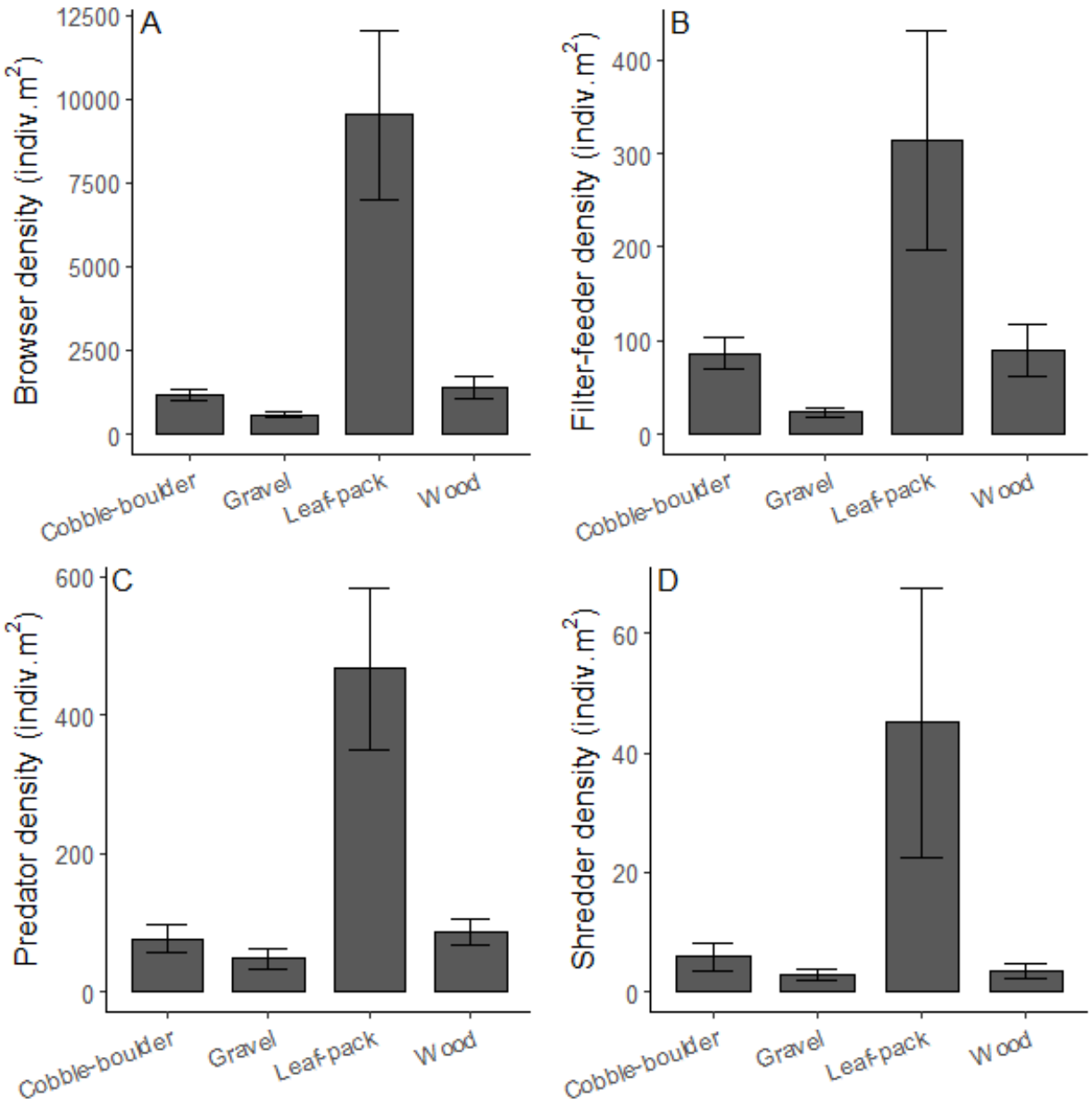

Figure 4. Major macroinvertebrate functional feeding group densities ($\bar{x}$ ± SE), amongst habitat types surveyed in 11 forested South Island streams. A, collector-browsers; B, filter-feeders; C, predators; D, shredders.

.

Table 5. Tukey's HSD post-hoc mean comparisons of common macroinvertebrate functional feeding group densities between in-stream habitat types surveyed in 11 forested South Island streams. * = significant; ** = very significant; *** = highly significant.

Feeding group	Habitat (I)	Habitat (J)	Mean difference (I-J)	Std. error	z	p
Collector-browsers						
	Leaf	Gravel	2.684	0.243	11.047	**<0.001*** **
	Wood	Leaf	-1.948	0.242	-8.049	**<0.001*** **
	Leaf	≥ Cobble	1.927	0.173	11.132	**<0.001*** **
	Gravel	≥ Cobble	-0.757	0.171	-4.437	**<0.001*** **
	Wood	Gravel	0.736	0.244	3.023	**<0.05***
	Wood	≥ Cobble	-0.020	0.172	-0.118	0.999
Filter-feeders						
	Leaf	Gravel	2.276	0.440	5.172	**<0.001*** **
	Wood	Leaf	-1.202	0.431	-2.792	**<0.05***
	Leaf	≥ Cobble	0.967	0.306	3.158	**<0.01****
	Gravel	≥ Cobble	-1.310	0.309	-4.241	**<0.001*** **
	Wood	Gravel	1.074	0.440	2.444	0.063
	Wood	≥ Cobble	-0.236	0.307	-0.769	0.856
Shredders						
	Wood	Leaf	-2.230	0.700	-3.186	**<0.01****
	Leaf	Gravel	2.159	0.758	2.850	**<0.05***
	Leaf	≥ Cobble	1.756	0.509	3.448	**<0.01****
	Wood	≥ Cobble	-0.474	0.521	-0.910	0.783
	Gravel	≥ Cobble	-0.404	0.550	-0.735	0.872
	Wood	Gravel	-0.070	0.770	-0.091	1.000
Predators						
	Leaf	Gravel	2.537	0.310	8.189	**<0.001*** **
	Leaf	≥ Cobble	1.941	0.217	8.957	**<0.001*** **
	Wood	Leaf	-1.763	0.305	-5.792	**<0.001*** **
	Wood	Gravel	0.774	0.312	2.483	0.057
	Gravel	≥ Cobble	-0.597	0.221	-2.702	**<0.05***
	Wood	≥ Cobble	0.177	0.217	0.818	0.832

Not surprisingly, variation in macroinvertebrate community assemblages corresponded with variation in functional feeding group densities between habitat types. All habitat types were numerically dominated by collector-browsers, filter-feeders and predators had intermediate

densities and varied relative to habitat type, whereas shredders were comparatively scarce (Figure 4). Leaf-packs had significantly the highest densities of all functional feeding groups (Table 5). Cobble-boulders and wood were intermediate, and varied little in functional feeding group densities, but both had significantly higher densities of collector-browser, filter-feeder, and predator feeding groups compared to gravel patches. Variation in shredder densities between cobble-boulders, wood, and gravel patches was non-significant ($p>0.05$). The taxonomic richness of collector-browsers and predators similarly varied between habitats (Figure 5). Collector-browser richness was significantly lower on gravel patches relative to other habitat types (leaf-packs – gravel patches ($b = 0.35$, $SE = 0.1$, $z = 3.6$, $p <0.01$); gravel patches – cobble-boulders ($b = -0.25$, $SE = 0.07$, $z = -3.5$, $p <0.01$); woody debris – gravel patches ($b = 3.1$, $SE = 0.1$, $z = 3.26$, $p <0.01$)); while predator richness was significantly higher on leaf-packs relative to gravel patches (leaf-packs – gravel patches ($b = 0.46$, $SE = 0.18$, $z = 2.58$, $p <0.05$)).

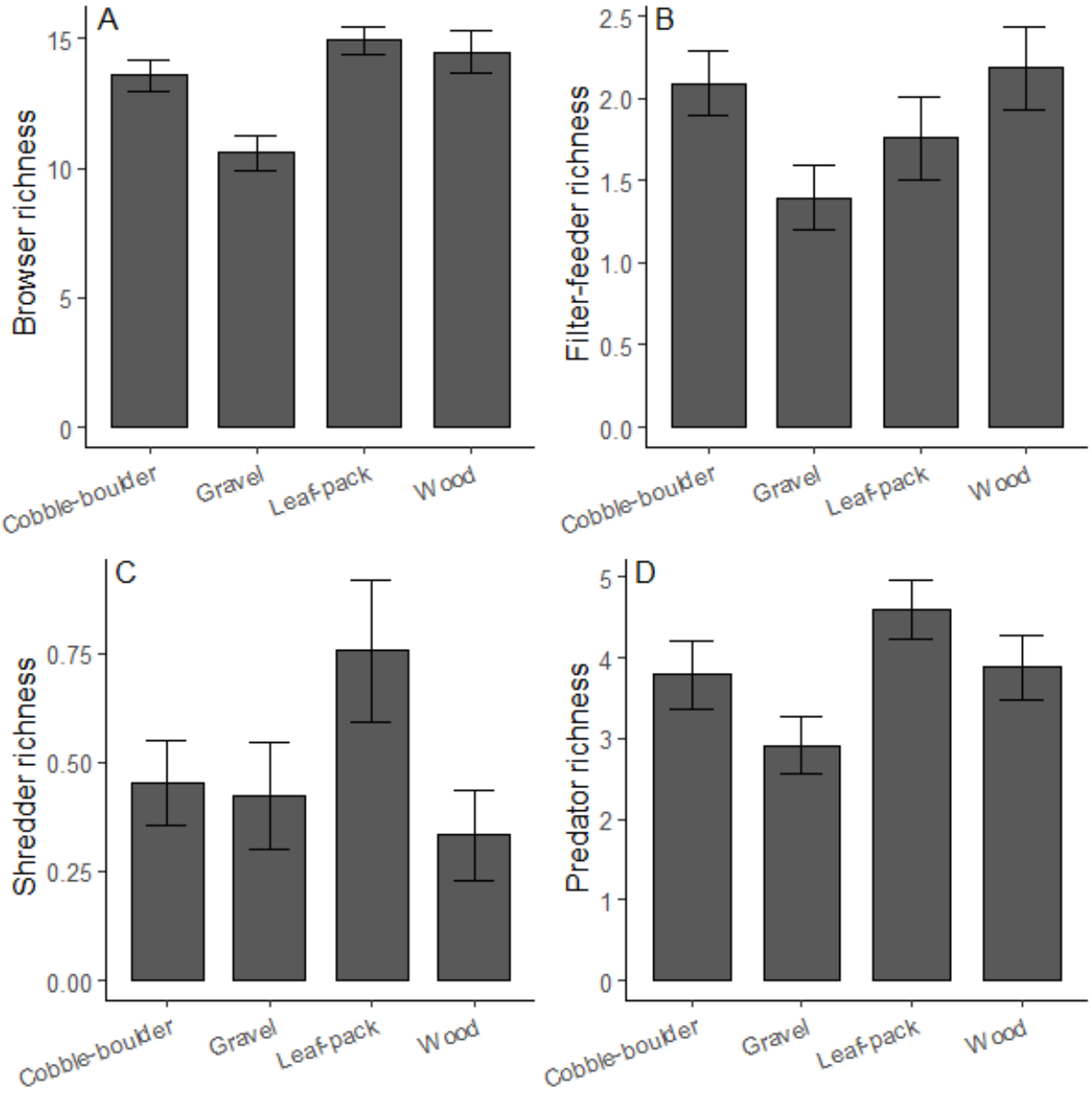

Figure 5. Taxonomic richness scores ($\bar{x}$ ± SE) for major functional feeding groups amongst in-stream habitat types surveyed in 11 forested South Island streams. A, collector-browsers; B, filter-feeders; C, shredders; D, predators.

Habitat addition experiment

Across the three waterways used for the habitat addition experiment, physical in-stream conditions (i.e. stream width, depth, velocity, and substrate size) were relatively consistent (Table 6). Additionally, water chemistry measurements were mostly consistent, although specific

Table 6. Reach-scale physico-chemical conditions across experimental (exp.) and control (cont.) reaches within study sites.

Physico-chemical parameter	Easterbrook		Ivan's drain		Fernside	
	Exp.	*Cont.*	*Exp.*	*Cont.*	*Exp.*	*Cont.*
Mean wetted width (m)	2.18	2.07	2.46	2.69	2.61	2.45
Mean depth (m)	0.21	0.22	0.18	0.17	0.21	0.21
Mean velocity (m s^{-1})	0.09	0.07	0.17	0.17	0.19	0.20
Mean substrate size (mm)	11	13	7	12	15	25
Fine sediment (%)	40	33	67	43	27	23
Temperature ($^{\circ}$C)	14	14	15	15	17	17
D.O (mg L^{-1})	8.3	8.3	5.9	5.9	8.6	8.6
pH	6.8	6.8	6.7	6.7	6.9	6.9
Conductivity (μS cm^{-1})	128	128	241	241	135	135

conductivity measurements in Ivan's Drain were almost 2-fold that of other waterways (Table 6). Based on width axis measurements, habitat additions were on average c.10-fold larger than bed substrate pebbles across all sites.

A total of 52 macroinvertebrate taxa were identified across all habitats, of which 45 were on cobble-boulders, 44 on control patches, and 41 on wood. Cobble-boulder additions had the highest average taxonomic richness (17.39 ± 0.72 SE), followed by wood (17.35 ± 0.73 SE), and control patches (14.72 ± 0.74 SE) (Figure 6A). Macroinvertebrate abundances followed a similar trend, with mean values highest on wood additions (880 ± 103 SE), followed by cobble-boulders (679 ± 74 SE), and control patches (353 ± 46 SE) (Figure 6B). However, mean Shannon-Wiener diversity values indicated that wood additions had relatively uneven compositions (1.57 ± 0.05 SE), compared to cobble-boulder additions (1.8 ± 0.06 SE) and control patches (1.65 ± 0.08 SE) (Figure 6C).

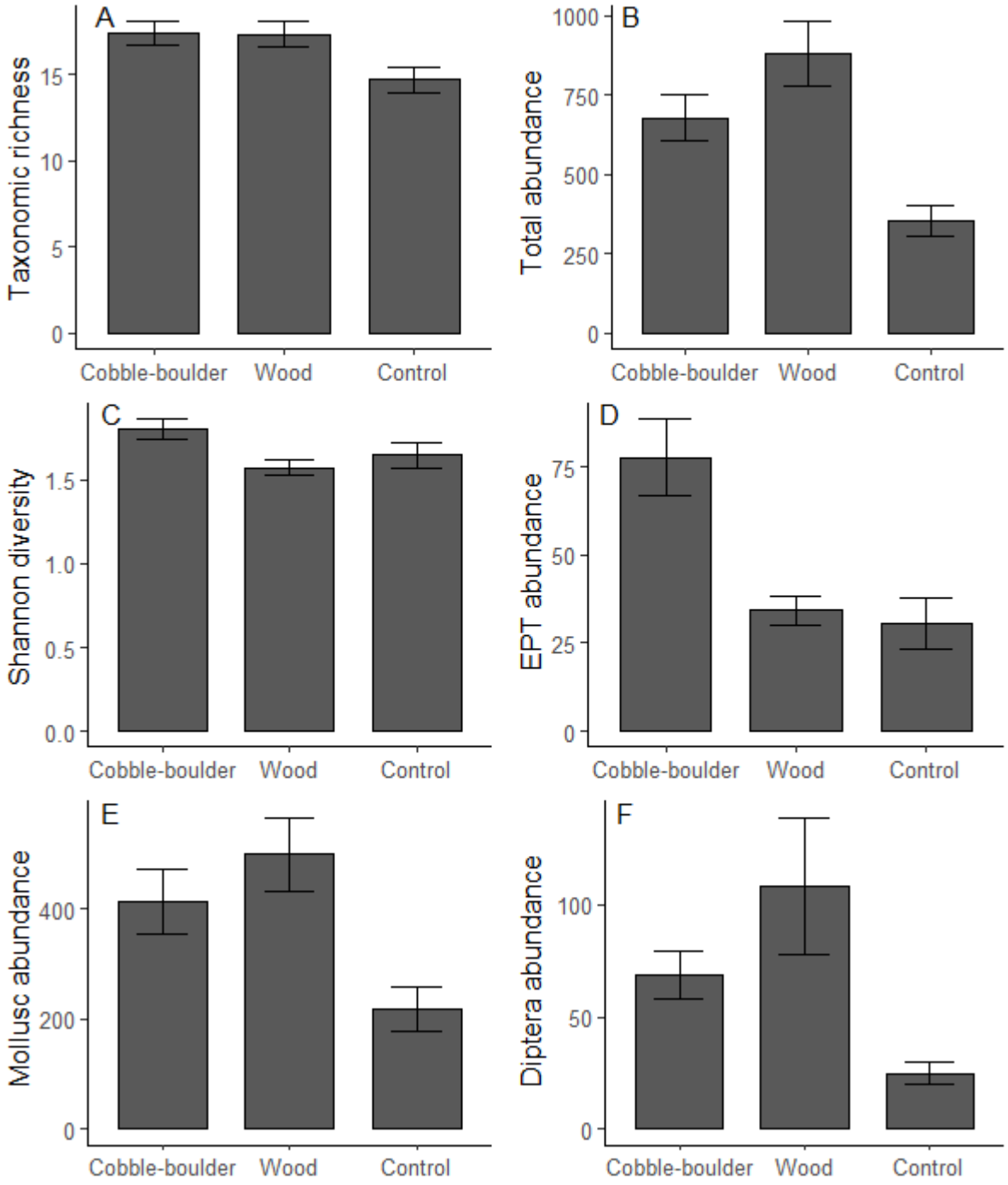

Figure 6. Macroinvertebrate distribution ($\bar{x}$ ± SE) across several community compositional metrics, amongst cobble-boulder and wood habitat additions, and control patches in three experimental waterways. A, total macroinvertebrate richness; B, total macroinvertebrate abundances; C, Shannon-Wiener diversity; D, EPT (pooled Ephemeroptera, Plecoptera, and Trichoptera) abundances; E, mollusc abundances; and F, dipteran abundances.

ANOSIM showed that community compositional variance was limited, although significant between all habitats. Variance was greatest between wood and control patches ($R = 0.22$, $p < 0.01$), followed by cobble-boulders and control patches ($R = 0.10$, $p < 0.01$), and cobble-boulders and wood ($R = 0.05$, $p < 0.05$). Taxonomic richness did not significantly differ between habitat additions and controls ($p > 0.05$). However, additions had significantly higher abundances than control patches (controls – cobble-boulders ($b = -0.67$, $SE = 0.16$, $z = -4.29$, $p < 0.001$); wood - controls ($b = 0.91$, $SE = 0.22$, $z = 4.07$, $p < 0.001$)). Variation between habitat additions types was non-significant ($p > 0.05$). Cobble-boulders had significantly higher Shannon-Wiener diversity values than wood (wood – cobble-boulder ($b = -0.23$, $SE = 0.09$, $z = -2.62$, $p < 0.05$)); yet neither treatments significantly differed from controls ($p > 0.05$).

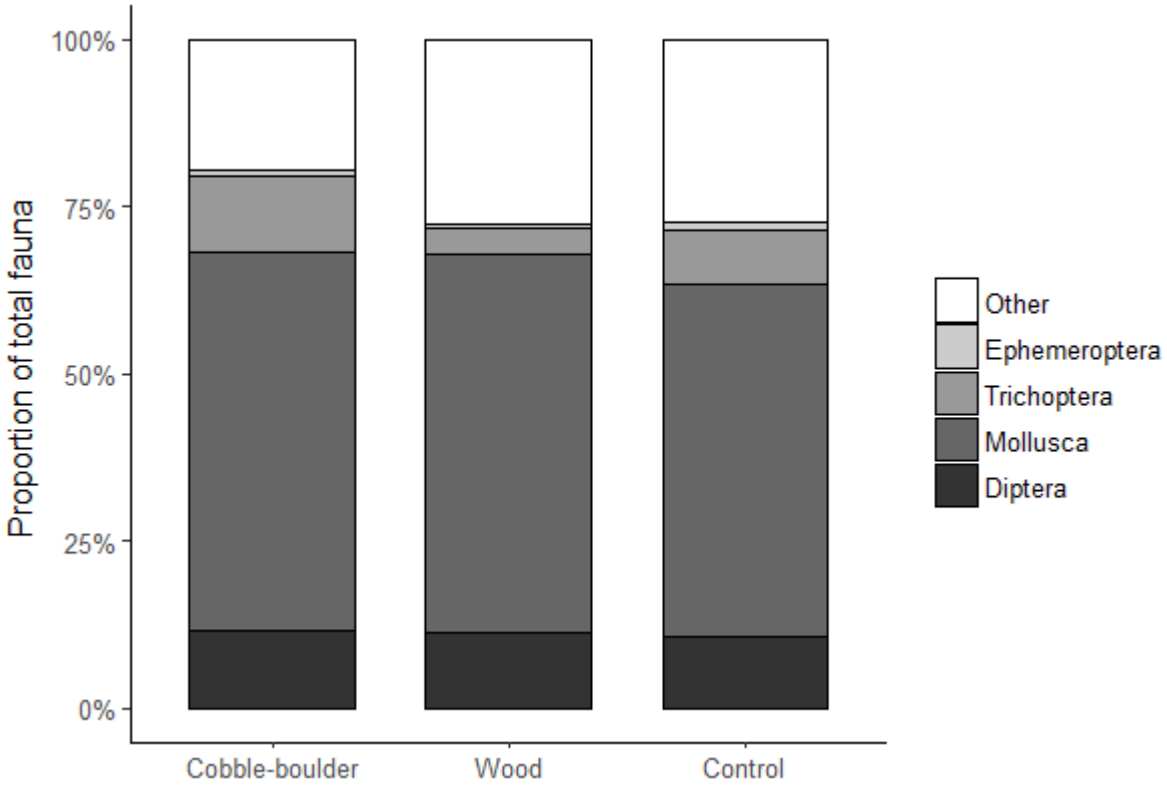

Figure 7. Proportions of common taxa sampled on cobble-boulder and wood additions, and control patches in three experimental waterways.

Proportionate order-level community compositions were similar amongst habitat additions and controls. Both were consistently dominated by molluscs with low ephemeropteran abundances, and plecopterans were absent (Figure 7). Neither habitat additions significantly improved the within-group richness of EPT, mollusc, or dipteran taxa relative to controls ($p>0.05$). However, these taxa were significantly more abundant on cobble-boulder additions, as were mollusc and dipteran abundances on wood additions, relative to controls (Table 7).

Table 7. Tukey's HSD post-hoc mean comparisons of common macroinvertebrate order abundances (EPT = pooled Ephemeroptera, Plecoptera, and Trichoptera) between in-stream habitat additions (wood and cobble-boulders), and gravel bed controls in three experimental waterways. * = significant; ** = very significant; *** = highly significant.

Taxa group	Habitat (I)	Habitat (J)	Mean difference (I-J)	Std. error	z	p
EPT						
	Control	≥Cobble	-0.935	0.220	-4.245	**<0.001*** **
	Wood	≥Cobble	-0.819	0.223	-3.673	**<0.001*** **
	Wood	Control	0.116	0.315	0.367	0.925
Mollusc						
	Wood	Control	0.849	0.315	2.696	**<0.05***
	Control	≥Cobble	-0.675	0.222	-3.044	**<0.01****
	Wood	≥Cobble	0.174	0.223	0.779	0.704
Diptera						
	Wood	Control	1.253	0.369	3.395	**<0.01****
	Control	≥Cobble	-1.233	0.253	-4.870	**<0.001*** **
	Wood	≥Cobble	0.021	0.259	0.079	0.996

All habitat types were numerically dominated by the collector-browser functional feeding group, followed by predators, filter-feeders, and shredders which were comparatively scarce (Figure 8). Within-group taxonomic richness did not significantly vary between habitat additions and controls ($p>0.05$). However, abundances did. Habitat additions had significantly higher

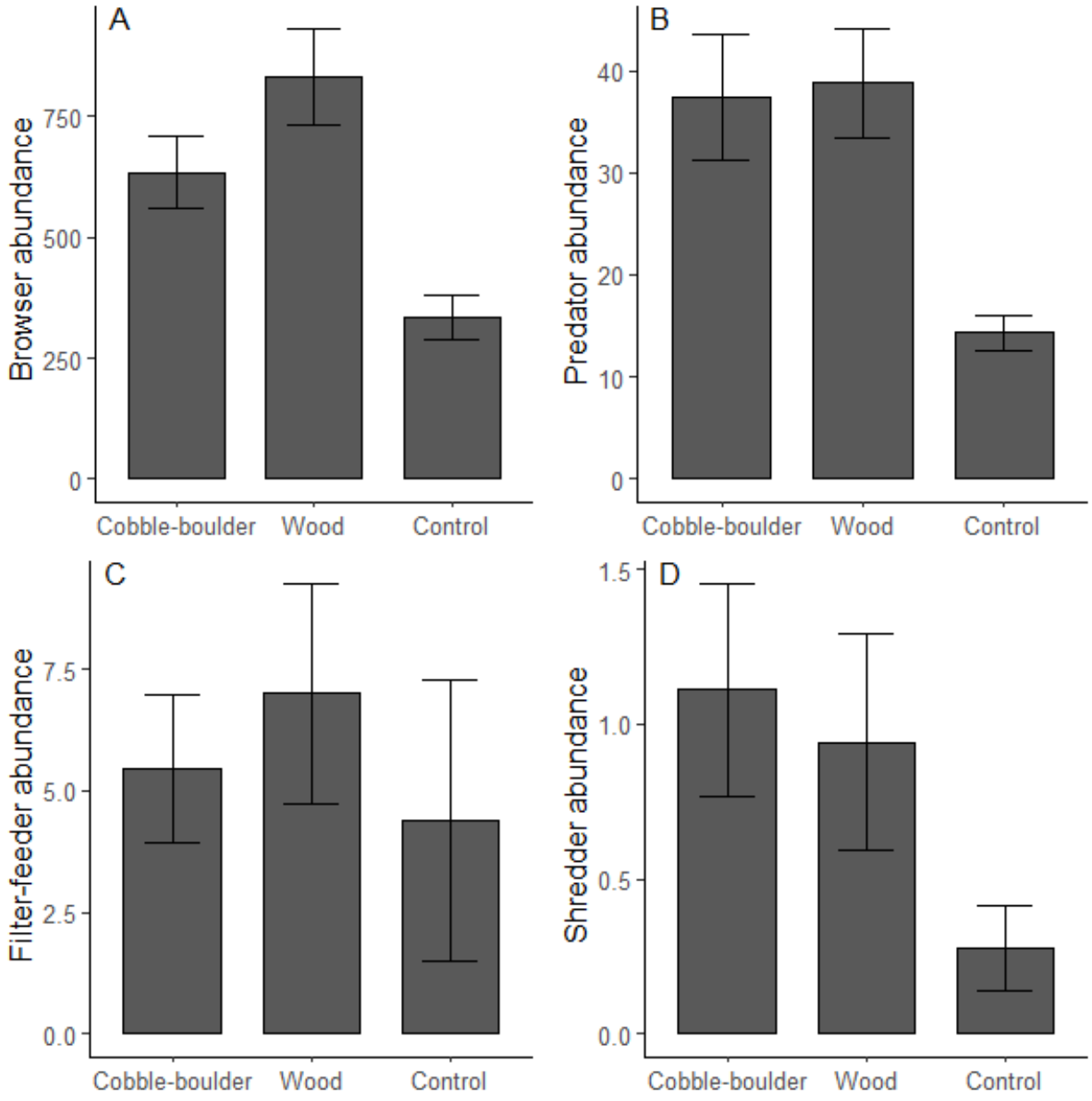

Figure 8. Abundance scores ($\bar{x}$ ± SE) for in-stream macroinvertebrate functional feeding groups amongst cobble-boulder and wood habitat additions and control patches in three experimental waterways. A, collector-browsers; B, predators; C, filter-feeders; and D, shredders.

collector-browser and predator abundances than control patches (Table 8). Although, the less abundant filter-feeder and shredder groups did not significantly differ between additions and controls ($p>0.05$).

Table 8. Tukey's HSD post-hoc mean comparisons of common macroinvertebrate functional feeding group abundances (collector-browser, filter-feeder, shredder, and predator) between in-stream habitat additions (wood and cobble-boulders), and gravel bed controls in three lowland Canterbury waterways. * = significant; ** = very significant; *** = highly significant.

Feeding group	Habitat (I)	Habitat (J)	Mean difference (I-J)	Std. error	z	p
Collector-browsers						
	Wood	Control	0.909	0.238	3.818	**<0.001*** **
	Control	≥Cobble	-0.658	0.167	-3.936	**<0.001*** **
	Wood	≥Cobble	0.251	0.169	1.479	0.288
Filter-feeders						
	Control	≥Cobble	-0.762	0.421	-1.811	0.158
	Wood	Control	0.351	0.584	0.602	0.812
	Wood	≥Cobble	-0.411	0.428	-0.960	0.591
Shredders						
	Control	≥Cobble	-1.389	0.641	-2.166	0.071
	Wood	Control	1.243	0.861	1.444	0.301
	Wood	≥Cobble	-0.146	0.544	-0.269	0.958
Predators						
	Wood	Control	0.995	0.275	3.617	**<0.001*** **
	Control	≥Cobble	-0.960	0.196	-4.891	**<0.001*** **
	Wood	≥Cobble	0.035	0.193	0.180	0.981

Discussion

The main objective for this study was to determine whether benthic macroinvertebrate communities vary between in-stream habitat types in forested South Island streams, and to assess whether the addition of cobble-boulder and wood habitat to lowland Canterbury waterways would result in improved benthic macroinvertebrate communities.

Riparian restoration is the most common practice being conducted in New Zealand to restore streams (McKergow et al. 2016). One of the ways that this method is expected to improve the health of the recipient stream is by reestablishing the connection between the aquatic and

surrounding terrestrial ecosystems through allochthonous wood and leaf-litter inputs. These inputs are expected to provide important habitat for in-stream biota, including the benthic macroinvertebrate fauna (Collier & Halliday 2000; Collier & Smith 2003; Parkyn & Collier 2004; Parkyn et al. 2009). However, it may be several decades until riparian plantings begin reintroducing woody debris to associated waterways (Meleason & Hall 2005; Davies-Colley et al. 2009), and some evidence indicates an absence of woody species in many riparian restoration projects in New Zealand (Jones et al. 2016). Additionally, there are currently no New Zealand published studies that explore the efficacy of in-stream habitat additions as a restoration tool in lowland waterways, and assumed benefits are entirely based on field surveys in unaltered waterways, and overseas research. My research thus addresses a critical knowledge gap on the role that in-stream habitat additions can offer to improve biodiversity and ecological functioning in degraded waterways. From my study, it will be clearer whether in-stream habitat availability is a factor currently limiting the recovery of benthic fauna in lowland Canterbury. Thereby, the often cited disconnect between restoration theory and practice may be partially alleviated (Lake 2001; Lake et al. 2007; Palmer et al. 2010), as local restoration targets can be more informed by local empirical evidence instead of anecdotes and extrapolations.

From my field survey, it was clear that in-stream habitat heterogeneity has an important role in the spatial distribution of benthic macroinvertebrate communities in forested South Island streams. This was evident from ANOSIM results, which showed that community compositions were highly dissimilar between some habitat types. Dissimilarity was particularly high between organic (i.e. leaf-packs and wood) and gravel habitats. This was a noteworthy finding, as gravel patches were treated as a control in this survey as they best represent the bed substrate in lowland Canterbury waterways. Collier and Halliday (2000) found a similar disparity in North Island

pumice-bed streams, attributing this to woody debris providing a trophic subsidy, and disturbance refugia for some taxa. Cobble-boulder, wood, and leaf-pack habitats all had significantly higher mean total taxonomic richness values than gravel patches. Furthermore, cobble-boulders appeared to be important habitat for rich EPT assemblages, while organic substrates (woody debris and leaf-packs) had richer dipteran communities, relative to gravel patches. Leaf-packs had a significantly higher richness of collector-browser and predator functional feeding groups, and cobble-boulders and wood had a significantly higher richness of collector browsers, than gravel patches. Gravel patches also had significantly the lowest total macroinvertebrate densities, and densities were usually the lowest amongst community compositional metrics and functional feeding groups. However, mean filter-feeder and predator densities did not significantly differ between woody debris and gravel patches, nor did shredder densities significantly differ between cobble-boulders, woody debris, and gravel patches. Functional feeding group richness was less distinct between habitat types, but gravel patches had significantly lower collector-browser richness than the other habitats sampled, and significantly lower predator richness than leaf-packs. Gravel patches similarly had significantly lower Shannon-Weiner diversity values than cobble-boulders and wood but did not significantly differ from leaf-packs which were also significantly less diverse than cobble-boulders.

These results were consistent with several lines of ecological theory. Gravel patches consist of an abundance of small pebbles, which are often easily mobilized during spates (Matthaei et al. 1999). Thus, resident communities are likely disproportionately susceptible to disturbance events. Matthaei et al. (2000) found that stable river-bed substrate (i.e. cobble-boulders and woody debris in my survey) provide refugia for disturbance susceptible taxa, and correspondingly had higher resident macroinvertebrate community density and richness.

Surprisingly, woody debris and cobble-boulders did not significantly differ in mean values of either community compositional, or functional feeding group metrics. This result was inconsistent with Collier and Halliday (2000), who found that communities differentiated between *Pinus radiata* and inorganic substrates partly based on feeding preferences. However, significant marginal variation following ANOSIM indicates that variation between these habitats may have occurred at a lower taxonomic level than considered in my analysis. Notwithstanding, increases in resident community density and richness as inorganic substrate size increases are well documented in the New Zealand literature (Jowett & Richardson 1990; Quinn & Hickey 1990; Jowett et al. 1991), a relationship that my results would suggest is consistent with wood. Leaf-pack habitats had mean total density values an order of magnitude greater than the other habitats considered in this survey. This result was expected, as leaf-packs were clearly more permeable than the other habitats sampled, and improved complexity is frequently attributed to more abundant and rich macroinvertebrate communities (Taniguchi & Tokeshi 2004; Thomaz et al. 2008). However, these habitats did not differ from cobble-boulders and wood across any taxonomic richness metrics. Collier and Smith (2003) found that leaf-packs (pine needles) break down at a rate 61-fold that of wood blocks of the same species, of which 43% was attributed to microbial processes. Correspondingly, respiration rates for leaf-packs were 20-fold those of wood blocks (Collier & Smith 2003). It is thus likely that the chemical habitat associated with leaf-packs (especially towards the center of the mass) is degraded relative to other hard-surfaced substrates (i.e. low dissolved oxygen) (Stotzky 1965). With this considered, it is not surprising that leaf-packs were proportionately dominated by tolerant detritivores (mostly chironomids), and consequentially had low Shannon-Weiner diversity scores. Albeit, as densities of all order-

level and functional feeding groups assessed were highest on leaf-packs, it is difficult to refute that these habitats are hotspots for secondary productivity in forested New Zealand waterways.

Leaf-packs were not considered in my habitat addition experiment. Due to the increased rate that leaf-packs are processed by in-stream fauna (i.e. Collier and Smith (2003) found that *Pinus radiata* needles were entirely processed in 176 days, a rate 61-fold that of wood blocks of the same species), comparisons between leaf-packs and hard-surfaced habitats following c.120 days of emmersion were deemed innapropriate for this experiment. However, patterns in the macroinvertebrate distribution between cobble-boulder, wood, and gravel (control) habitats in lowland Canterbury waterways generally reflected patterns found in forested South Island waterways, and were likely derrived from similar mechanisms. Total abundances were consistently higher on cobble-boulder and wood additions relative to gravel patch controls. Similarly, EPT and collector-browser density, and filter-feeder, shredder, and predator richness patterns were similar between survey streams and experimental treatments. However, unlike in forested South Island waterways, cobble-boulder additions did not significantly improve filter-feeder abundances, yet wood additions did significantly improve predator abundances in lowland experiment sites. Additionally, a more disconcerting disparity was that neither habitat additions significantly improved any macroinvertebrate richness values. This result contrast those of Lester et al. (2007), who found that wood additions in Australian agricultural streams improved invertebrate densities, taxonomic and functional diversity, and numbers of taxa sensitive to disturbance, relative to benthic and edge habitats. This finding also contrasts a meta-analysis conducted by Miller et al. (2010), that found wood and boulder habitat additions generally increase invertebrate richness, yet not density relative to controls. However, this was consistent

with a less targeted meta-analysis of local habitat restoration (i.e. inclusive of a wider range of habitat restoration procedures) (Palmer et al. 2010).

Although restoration in the strictest sense (i.e. to a pre-degraded state) is not considered as a feasible endpoint for most studies, there were likely several key constraints that limited the efficacy of my habitat additions to improve community compositions in lowland Canterbury waterways. Additionally, due to unforeseen circumstances limiting the number of sites available to conduct this experiment, several minor or less consistent invertebrate responses to habitat additions may not have provided statistically significant results. Notwithstanding, the number of habitat additions made to each stream may have been insufficient to trigger a significant response from rare taxa. Lester et al. (2007) found positive reach-scale effects on benthic community diversity in Australian agricultural waterways by mimicking local reference wood loads from nearby unimpaired waterways (i.e. 71 locally sourced indigenous tree branches of various sizes per 50 m reach) and positioning additions in natural assortments (i.e. both log jams and stand-alone branches). Additionally, Lester et al. (2007) allowed wood additions to stand for 6 months before sampling. This timescale was unfeasible for this and many restoration projects, yet likely has important implications (Moreno-Mateos et al. 2012; Jones et al. 2018). Collier and Smith (2003) documented an 84-day emersion period before phytophagus caddisflies began directly feeding on *Pinus radiata* blocks, indicating that the potential for wood block additions to provide a trophic subsidy in my experiment may not have been entirely realised within the emersion times allocated in my experiment. The importance of restoration time-frames was emphasised by Harding et al. (1998), who found that decades-old watershed land-use practices were the best predictor of in-stream biodiversity, while later alterations to land-use (i.e. <10-year-old riparian and watershed reforestation) were comparatively poor. Furthermore, landscape-scale processes

likely strongly influenced the pool of species able to disperse to my restoration sites (Poff 1997; Parkyn & Smith 2011). Palmer et al. (2010) attributed a failure by practitioners to consider landscape-scale processes when restoring waterways as the key factor limiting the perceived success of stream restoration projects worldwide. This is an especially important consideration for restoring benthic communities in lowland Canterbury waterways, as both aquatic habitats (i.e. larval insect habitat) and terrestrial habitats (i.e. dispersing adult insect habitat) have become degraded at a regional scale (Harding & Winterbourn 1995; Quinn et al. 1997; Petersen et al. 2004; Ewers et al. 2006; Winterbourn et al. 2007; Didham et al. 2012). In conjunction, I did not address limitations on local oviposition habitat. Thus, it is likely that the prospect of restoring macroinvertebrate communities in my experimental waterways was limited to improving or redistributing current in-stream populations.

Given the extent of factors I attributed to the shortcomings/limitations/practical limitations of this study, avenues for future research are clear. Increasing the number of study sites and in-stream habitat additions, and longer permitted monitoring timeframes would alleviate uncertainty regarding whether the primary factors limiting perceived restoration success are derived from shortcomings in restoration practices, or experimental design and monitoring procedure. More importantly, deforestation and land-use change is widespread in the Canterbury region, and terrestrial and aquatic insect habitats are consequentially degraded (Ewers et al. 2006). Local habitat restoration projects are therefore likely to be highly limited in restoring stream invertebrate communities, as dispersal is limited by extensive areas of poor habitat (Harding & Winterbourn 1995; Quinn et al. 1997; Hall et al. 2001; Petersen et al. 2004; Winterbourn et al. 2007; Didham et al. 2012). Thus, future restoration must shift focus from conducting isolated local habitat restorations, to reestablishing connectivity between forested and

anthropogenic landscapes. As detailed by Poff (1997), and emphasised by Palmer et al. (2010), local biotic recovery is limited by a spatial hierarchy of constraints, beginning with the factors that limit regional species pools. Restoration must therefore target constraints at the largest spatial scales first. In doing so, creating a foundation to more effectively test restoration practices at lower spatial scales.

This study provides empirical evidence regarding the efficacy of two types of in-stream habitat additions for restoring benthic macroinvertebrate communities in lowland Canterbury waterways. My results lead me to conclude that cobble-boulder and wood habitat additions are currently a highly limited restoration tool in lowland Canterbury waterways, but could have potential when combined with a suite of large-scale management actions in addition to riparian management. In the timeframe permitted for this study, cobble-boulders and wood appeared to have similar efficacy as stream restoration tools, and relatively high resident abundances of several taxonomic and functional feeding groups indicated that these substrates may provide improved refugia relative to *status quo* gravel bed habitat. However, given the depauperate benthic fauna in these waterways, and the wide-scale degradation of aquatic and terrestrial habitats in lowland Canterbury, it was not surprising that these additions failed to improve any community diversity metrics.

References

Armstrong RA 2014. When to use the Bonferroni correction. Ophthalmic and Physiological Optics 34(5): 502-508.

Bachman RA 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113(1): 1-32.

Bates D, Maechler M, Bolker B, Walker S 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1(7): 1-23.

Bernhardt ES, Palmer MA, Allan J, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J 2005. Synthesizing US river restoration efforts. Science 308(5722): 636-637.

Bernhardt ES, Sudduth EB, Palmer MA, Allan JD, Meyer JL, Alexander G, Follastad-Shah J, Hassett B, Jenkinson R, Lave R 2007. Restoring rivers one reach at a time: results from a survey of US river restoration practitioners. Restoration Ecology 15(3): 482-493.
Burdon FJ, McIntosh AR, Harding JS 2013. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. Ecological Applications 23(5): 1036-1047.
Burrell TK, O'Brien JM, Graham SE, Simon KS, Harding JS, McIntosh AR 2014. Riparian shading mitigates stream eutrophication in agricultural catchments. Freshwater Science 33(1): 73-84.
Collier K 1993. Review of the status, distribution, and conservation of freshwater invertebrates in New Zealand. New Zealand journal of marine and freshwater research 27(3): 339-356.
Collier KJ, Halliday JN 2000. Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: stable habitat or trophic subsidy? Journal of the North American Benthological Society 19(1): 94-111.
Collier KJ, Smith BJ 2003. Role of wood in pumice-bed streams: II: Breakdown and colonisation. Forest Ecology and Management 177(1-3): 261-276.
Collier KJ, Aldridge BM, Hicks BJ, Kelly J, Macdonald A, Smith BJ, Tonkin J 2009. Ecological values of Hamilton urban streams (North Island, New Zealand): constraints and opportunities for restoration. New Zealand Journal of Ecology: 177-189.
Collins KE, Doscher C, Rennie HG, Ross JG 2013. The effectiveness of riparian 'restoration'on water quality—a case study of lowland streams in Canterbury, New Zealand. Restoration Ecology 21(1): 40-48.
Cowie B 1980. Community dynamics of the bethnic fauna in a West Coast stream ecosystem.
Davies-Colley RJ, Meleason MA, Hall RM, Rutherford JC 2009. Modelling the time course of shade, temperature, and wood recovery in streams with riparian forest restoration. New Zealand Journal of Marine and Freshwater Research 43(3): 673-688.
Didham RK, Blakely TJ, Ewers RM, Hitchings TR, Ward JB, Winterbourn MJ 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundamental and Applied Limnology/Archiv für Hydrobiologie 180(1): 27-40.
Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK 2006. Past and future trajectories of forest loss in New Zealand. Biological Conservation 133(3): 312-325.
Foote KJ, Joy MK, Death RG 2015. New Zealand dairy farming: milking our environment for all its worth. Environmental management 56(3): 709-720.
Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27(2): 233-249.
Graham A, McCaughan D, McKee F 1988. Measurement of surface area of stones. Hydrobiologia 157(1): 85-87.
Graynoth E, Sagar P, Taylor MJ 1993. Effects of the Wilberforce Diversion on the benthic fauna and fish stocks of Lake Coleridge, NIWA Freshwater.
Greenwood MJ, Harding JS, Niyogi DK, McIntosh AR 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. Journal of Applied Ecology 49(1): 213-222.
Grimm NB 1988. Role of macroinvertebrates in nitrogen dynamics of a desert stream. Ecology 69(6): 1884-1893.

Hall MJ, Closs GP, Riley RH 2001. Relationships between land use and stream invertebrate community structure in a South Island, New Zealand, coastal stream catchment. New Zealand Journal of Marine and Freshwater Research 35(3): 591-603.
Harding J, Benfield E, Bolstad P, Helfman G, Jones E 1998. Stream biodiversity: the ghost of land use past. Proceedings of the national academy of sciences 95(25): 14843-14847.
Harding JS, Winterbourn MJ 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. New Zealand journal of marine and freshwater research 29(4): 479-492.
Hill MO 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54(2): 427-432.
Hynes H 1975. The stream and its valley: With 4 figures and 2 tables in the text. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 19(1): 1-15.
Jones H, Kimberley M, Hill R, Borman D 2016. Riparian Characteristics of Pastoral Waterways in the Waikato Region, 2002-2012.
Jones HP, Jones PC, Barbier EB, Blackburn RC, Benayas JMR, Holl KD, McCrackin M, Meli P, Montoya D, Mateos DM 2018. Restoration and repair of Earth's damaged ecosystems. Proc. R. Soc. B 285(1873): 20172577.
Jowett IG, Richardson J 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for Deleatidium spp. New Zealand journal of marine and freshwater research 24(1): 19-30.
Jowett IG, Richardson J, Biggs BJ, Hickey CW, Quinn JM 1991. Microhabitat preferences of benthic invertebrates and the development of generalised Deleatidium spp. habitat suitability curves, applied to four New Zealand rivers. New Zealand journal of marine and freshwater research 25(2): 187-199.
Lake P 2001. On the maturing of restoration: linking ecological research and restoration. Ecological Management & Restoration 2(2): 110-115.
Lake P, Bond N, Reich P 2007. Linking ecological theory with stream restoration. Freshwater biology 52(4): 597-615.
Lester RE, Wright W, Jones-Lennon M 2007. Does adding wood to agricultural streams enhance biodiversity? An experimental approach. Marine and Freshwater Research 58(8): 687-698.
Manaaki Whenua - Landcare Research 2018. Identification guide: What freshwater invertebrate is this? https://www.landcareresearch.co.nz/resources/identification/animals/freshwater-invertebrates/guide
Matthaei CD, Peacock KA, Townsend CR 1999. Patchy surface stone movement during disturbance in a New Zealand stream and its potential significance for the fauna. Limnology and Oceanography 44(4): 1091-1102.
Matthaei CD, Arbuckle CJ, Townsend CR 2000. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. Journal of the North American Benthological Society 19(1): 82-93.
McDowall R 1965. Studies on the biology of the red-finned bully Gobiomorphus huttoni (Ogilby). 3. Food studies. Transactions Roy. Soc. NZ 5: 233-254.
McDowall RM 1968. Galaxias maculatus (Jenyns), the New Zealand whitebait, Fisheries Research Division, Marine Department.
McDowall RM 1990. New Zealand freshwater fishes: a natural history and guide.

McDowell R, Larned S, Houlbrooke D 2009. Nitrogen and phosphorus in New Zealand streams and rivers: control and impact of eutrophication and the influence of land management. New Zealand Journal of Marine and Freshwater Research 43(4): 985-995.
McKergow LA, Matheson FE, Quinn JM 2016. Riparian management: A restoration tool for New Zealand streams. Ecological Management & Restoration 17(3): 218-227.
Meleason MA, Hall GM 2005. Managing plantation forests to provide short-to long-term supplies of wood to streams: a simulation study using New Zealand's pine plantations. Environmental Management 36(2): 258-271.
Miller SW, Budy P, Schmidt JC 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. Restoration Ecology 18(1): 8-19.
Moreno-Mateos D, Power ME, Comín FA, Yockteng R 2012. Structural and functional loss in restored wetland ecosystems. PLoS biology 10(1): e1001247.
Mulholland PJ, Newbold JD, Elwood JW, Hom CL 1983. The effect of grazing intensity on phosphorus spiralling in autotropic streams. Oecologia 58(3): 358-366.
Negishi J, Inoue M, Nunokawa M 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. Freshwater Biology 47(8): 1515-1529.
Oksanen J, Blanchet FG, Kindt R, Legendre P, O'hara R, Simpson GL, Solymos P, Stevens MHH, Wagner H 2011. vegan: Community Ecology Package. R package version 1.17-2. R Foundation for Statistical Computing, Vienna. Available: CRAN. R-project. org/package= vegan.(July 2012).
Palmer MA, Ambrose RF, Poff NL 1997. Ecological theory and community restoration ecology. Restoration ecology 5(4): 291-300.
Palmer MA, Menninger HL, Bernhardt E 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 55: 205-222.
Parkyn SM, Collier KJ 2004. Interaction of press and pulse disturbance on crayfish populations: flood impacts in pasture and forest streams. Hydrobiologia 527(1): 113-124.
Parkyn SM, Smith BJ 2011. Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. Environmental management 48(3): 602-614.
Parkyn SM, Meleason MA, Davies-Colley RJ 2009. Wood enhances crayfish (Paranephrops planifrons) habitat in a forested stream. New Zealand Journal of Marine and Freshwater Research 43(3): 689-700.
Parkyn SM, Davies-Colley RJ, Halliday NJ, Costley KJ, Croker GF 2003. Planted riparian buffer zones in New Zealand: do they live up to expectations? Restoration ecology 11(4): 436-447.
Petersen I, Masters Z, Hildrew A, Ormerod SJ 2004. Dispersal of adult aquatic insects in catchments of differing land use. Journal of Applied Ecology 41(5): 934-950.
Poff NL 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the north american Benthological society: 391-409.
Quinn JM, Hickey CW 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. New Zealand journal of marine and freshwater research 24(3): 411-427.
Quinn JM, Phillips NR, Parkyn SM 2007. Factors influencing retention of coarse particulate organic matter in streams. Earth Surface Processes and Landforms 32(8): 1186-1203.

Quinn JM, Williamson RB, Smith RK, Vickers ML 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 2. Benthic invertebrates. New Zealand journal of marine and freshwater research 26(2): 259-273.
Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand journal of marine and freshwater research 31(5): 579-597.
Renouf K, Harding J 2015. Characterising riparian buffer zones of an agriculturally modified landscape. New Zealand journal of marine and freshwater research 49(3): 323-332.
Rowe D, Cudby E, Turner D 2000. Prey species and the food web for rainbow trout in Lake Rotoaira, 1972–1974. NIWA Client Report GPL00233. National Institute of Water and Atmospheric Research, Hamilton.
Sagar P, Eldon G 1983. Food and feeding of small fish in the Rakaia River, New Zealand. New Zealand journal of marine and freshwater research 17(3): 213-226.
Smith CM 1987. Sediment, phosphorus, and nitrogen in channelised surface run-off from a New Zealand pastoral catchment. New Zealand journal of marine and freshwater research 21(4): 627-639.
Statistics New Zealand 2012. Statistics New Zealand Infoshare
Stotzky G 1965. Microbial respiration. Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties(methodsofsoilanb): 1550-1572.
Symonds MR, Moussalli A 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65(1): 13-21.
Taniguchi H, Tokeshi M 2004. Effects of habitat complexity on benthic assemblages in a variable environment. Freshwater Biology 49(9): 1164-1178.
Team RC 2013. R: A language and environment for statistical computing.
Thomaz SM, Dibble ED, Evangelista LR, Higuti J, Bini LM 2008. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. Freshwater biology 53(2): 358-367.
Wilcock R, Monaghan R, Quinn J, Srinivasan M, Duncan M, Scarsbrook M 2013. Trends in water quality of five dairy farming streams in responses to changes in farm management and adoption of best practice: benefits of long-term monitoring at the catchment scale. Mar Freshw Res 64: 401-412.
Williamson RB, Smith RK, Quinn JM 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 1. Channel form and stability. New Zealand journal of marine and freshwater research 26(2): 241-258.
Winterbourn MJ, Gregson KL, Dolphin CH 1989. Guide to the aquatic insects of New Zealand, Entomological Society of New Zealand Auckland.
Winterbourn MJ, Chadderton WL, Entrekin SA, Tank JL, Harding JS 2007. Distribution and dispersal of adult stream insects in a heterogeneous montane environment. Fundamental and Applied Limnology/Archiv für Hydrobiologie 168(2): 127-135.
Wolman MG 1954. A method of sampling coarse river-bed material. EOS, Transactions American Geophysical Union 35(6): 951-956.

Chapter 3 - Determining factors affecting oviposition site selection by aquatic invertebrates

Introduction

The historic failings of stream restoration have been widely documented over recent decades; oftentimes attributed to a disconnect between ecological theory, and restoration practice (Lake et al. 2007; Palmer et al. 2010). Many past restoration efforts were conducted under the assumption that the restoration of in-stream and riparian habitat heterogeneity will restore the in-stream community assemblage. A 'Field of Dreams Hypothesis' (i.e. if you build it, they will come) (Palmer et al. 1997; Lake et al. 2007). The shortcomings of this approach have become increasingly apparent, and have been frequently documented in ecological literature (Palmer et al. 2010). As a result, many restoration efforts are now being encouraged to adopt a holistic approach to restoration, based on ecological theory and empirical evidence (Lake et al. 2007; Palmer et al. 2010). In doing so, restoration can target the factors which most constrain ecological restoration. Parkyn and Smith (2011) broadly identified these as dispersal, local habitat, and biotic constraints, all of which interact, and all of which are primarily influenced by limitations at the landscape scale. Building on this, Lake et al. (2007) proposed a restoration framework, highlighting the importance of considering: the life histories, habitat template, and spatio-temporal scope of target organisms; requirements of refugia relative to local environmental disturbance regimes; longitudinal and lateral connectivity; food-web structure; local assembly rules; successional mechanisms and pathways; ecosystem processes; and the spatial scale of restoration. Although contemporary restoration ecology is taking steps to

incorporate aspects of ecological theory, our understanding is limited by the absence of an evidence-based restoration 'tool-kit', detailing how constraints on restoration can be overcome. One constraint that requires further investigation are the factors that limit adult insect dispersal to restored sites.

Many of New Zealand's aquatic insects have complex life histories, temporally dominated by an aquatic larval life stage, and often with a winged adult dispersal stage (Collier & Winterbourn 2000). The laying of eggs and subsequent recruitment of larvae to generate in-stream populations is largely limited by insects' ability to successfully disperse and oviposit. Dispersal constraints are broadly derived from either environmental conditions, or species behaviour and traits (Parkyn & Smith 2011). In many cases, these two categories are linked. For example, in landscapes that have been largely developed through urbanisation or agriculture, the fragmentation of stream habitats can result in a loss of connectivity from source populations and subsequent extirpation of taxa with poor dispersal capabilities, while those with adaptations for long distance dispersal may not be effected (Harding et al. 1998; Parkyn & Smith 2011). Additionally, the presence of anthropogenic structures, such as road culverts and bridges, have been shown to disrupt the longitudinal connectivity of some stream insect populations (Blakely et al. 2006). In many cases, the remediation of large-scale dispersal constraints can be practically unfeasible over restoration timeframes (Winterbourn et al. 2007a; Parkyn & Smith 2011). However, it has long been recognised that there are a range of taxonomically specific oviposition strategies, some of which require particular habitats (Collier & Winterbourn 2000). Thus, in addition to the large-scale dispersal constraints which may limit the pool of species able to disperse to restoration sites, local species assemblages may also be limited by a lack of taxonomically specific oviposition habitat.

Catchment-scale aquatic insect population dynamics are first and foremost influenced by adult insects' ability to disperse eggs throughout the river system. However, whether the availability of taxonomically specific oviposition habitat can constrain oviposition has been an area of little research. In a Scottish study on *Baetis* mayflies, Lancaster et al. (2010) found that reaches with poor emergent boulder habitat availability received significantly fewer egg masses. This relationship has since been identified to affect subsequent reach-scale *Baetis* abundances (Encalada & Peckarsky 2012). In contrast, greater oviposition in habitat rich reaches did not correspond to significantly higher larval abundances of hydrobiosid caddisflies when compared to habitat poor reaches, in an Australian stream (Reich & Downes 2004). This may indicate that reaches with rich oviposition habitat are an important source of early instar larvae to those where oviposition habitat is poor.

Under the Preference Performance Hypothesis (PPH) (Jaenike 1978; Bovill et al. 2013), the oviposition strategy employed by adult insects should maximise the fitness of egg masses and thus the recruitment of larvae to the local population. However, as all oviposition strategies are not akin, the advantages to egg mass fitness by selectively choosing oviposition habitat are thought to vary between different strategies (Bovill et al. 2013). Insects that oviposit directly onto the water surface by using a 'bomber', 'splasher', or 'dipper' strategy (Encalada & Peckarsky 2007), such as many ephemeropterans in New Zealand (Winterbourn 1978) and globally (Encalada & Peckarsky 2007), are thought to have adapted little selectivity for within-stream oviposition habitat. This is because the consequences to egg mass fitness by selectively ovipositing are few due to the mobility of eggs in the water column (Bovill et al. 2013). Thus, the small-scale environmental conditions at the site of oviposition may have few consequences to the fitness of eggs. However, the consequences to egg mass fitness by taxon that use a 'lander'

strategy (Encalada & Peckarsky 2007), are thought to be significant (Bovill et al. 2013). Under this strategy, eggs are oviposited onto fixed structures such as bankside or aquatic plants (i.e. *Archichauliodes diversus* (Hamilton 1940), and *Xanthocnemis zealandica* (Rowe 1987)), or on the submerged surface of emergent in-stream substrate (i.e. *Baetis* Mayflies (Peckarsky et al. 2000); New Zealand simuliids (Storey et al. 2016); and Australasian hydrobiosids (Reich & Downes 2003b, a; Storey et al. 2016) in single masses. Egg masses are thus subject to the environmental conditions of their respective oviposition site, and likely face fitness consequences relative to these and the morphological/physiological characteristics of the egg mass. A maternal investment in selecting oviposition sites that will reduce environmental stress on egg masses would therefore be beneficial. These benefits have been studied for hydrobiosid caddisflies in Australia, where it was found that the selection of oviposition sites (emergent substrate) in slow flowing water by one species was due to the vulnerability of egg masses to shear stress in higher flows (Bovill et al. 2013). Similarly, lower egg mortality rates were observed for North American *Baetis* mayfly eggs oviposited on preferred habitat (Peckarsky et al. 2000). Thus, while abundance of oviposition habitat is an important determinant of the frequency of insect oviposition, the quality of oviposition habitat may determine the ultimate fitness of egg masses, and thus hatching success.

For research in this field to inform restoration practitioners and improve the quality of stream restoration, the physico-chemical/habitat conditions that constrain or improve oviposition must be identified. In a survey of two rivers in Victoria, Australia, Reich and Downes (2003b) found that the likelihood of most insect egg masses being oviposited on substrate was positively associated with substrate size, while some showed preferences for faster and slower flows. Similarly, in the Waikato region of New Zealand, Storey et al. (2016) found that hydrobiosids,

hydropsychids, and two *Austrosimulium* species selectively oviposited on larger, unembedded substrate with large emergent portions. However, in light of the inherent variability in regional environmental conditions and species pools (Poff 1997), and documented cases of species-level specificity for oviposition habitat (Reich & Downes 2003a; Bovill et al. 2013), it is evident that the oviposition habitat restoration 'tool kit' is not necessarily synonymous across regions.

Therefore, the main objective of my study was to determine whether in-stream habitat restoration can be tailored to maximise the diversity and abundance of insects ovipositing in lowland Canterbury waterways. Specifically, my first aim was to determine whether substrate characteristics, and the microhabitat-scale physico-chemical environmental conditions (immediately surrounding substrate) provide oviposition cues for winged adult aquatic insects.

My second aim was to quantify the surface complexity of distinctly smooth and rough surfaced substrate, and experimentally test the effect of substrate surface roughness on insect oviposition. An experimental approach was taken because this parameter was expected to be difficult to quantify in the field, as substrate surface roughness is largely influenced by large-scale environmental factors such as catchment-scale geology and hydrology, and distance from the sediment source. Thus, variation in within-reach substrate surface roughness was expected to be minimal in survey streams. The positive effects of complexity (i.e. the extent of habitats within a defined spatial scale) on biodiversity are frequently documented (Thomaz et al. 2008; Koivisto & Westerbom 2010; Palmer et al. 2010). Previous studies provide evidence that increased complexity can improve oviposition at the reach scale (Reich & Downes 2004; Lancaster et al. 2010). However, there is no evidence to indicate whether this relationship exists at the individual microhabitat scale. Substrate surface roughness is an indicator of microhabitat-scale complexity. For example, relative to smooth surfaced substrates, crevices and protrusions

on rough surfaced substrates create a wider variety of substrate surface conditions (i.e. variation in exposure to sheer stress). Given the suite of evidence connecting habitat complexity to biodiversity, I hypothesised that a more taxonomically rich assemblage of insects would oviposit on substrate with a more complex surface. Additionally, habitat complexity has been attributed to higher invertebrate densities for some stream invertebrate taxa, potentially due to refugia from predation (Diehl 1992) or flooding disturbance (Matthaei et al. 2000). While this relationship is supported for benthic life-stages, whether this is consistent with insect oviposition habitat preference is currently unclear. Personal field observations indicated this was the case. Therefore, I also hypothesised that microhabitat-scale surface complexity would increase the abundance of insect egg masses oviposited on substrate.

Methods

This study was conducted in two parts. Firstly, I undertook a field survey to investigate physico-chemical and habitat characteristics of oviposition sites. Secondly, I conducted a small-scale habitat addition experiment to test emergent substrate surface complexity as a selection criterion.

Field survey

I surveyed eight forested first to third order streams to assess aquatic invertebrate oviposition. Forested streams were selected to minimise the influence of anthropogenic land-use practices (i.e. high sediment, nutrient enrichment, and high temperatures (Quinn et al. 1997)). All streams were on Banks Peninsula, a 1,150 km^2 volcanic peninsula on the eastern coast of Canterbury, New Zealand. This area was selected due to its proximity to Christchurch, and abundance of remnant forest patches. Streams with poor roadside access, and few large emergent substrates were rejected.

Figure 9. Survey reach located in Pidgeon Bay Stream, Banks Peninsula. The reach had numerous large emergent boulders, riffle-run habitats and was heavily shaded. (Photo credit T. Green)

Survey reaches were located in the Kaituna River, Okuti River, Pigeon Bay Stream, an unnamed stream in Wainui Bay, Balguerie Stream, Narbey Stream, and two tributaries to Narbey Stream (T1 and T2) (Table 9).

Table 9. Survey site locations with GPS coordinates. T1 = tributary one; T2 = tributary two

Site	Latitude	Longitude
Kaituna River	-43.742747°	172.687054°
Okuti River	-43.785462°	172.832876°
Pigeon Bay Stream	-43.702594°	172.897853°
Wainui Bay	-43.812257°	172.894453°
Balguerie Stream	-43.820618°	172.988612°
Narbey Stream	-43.493526°	173.23805°
Narbey Stream (T1)	-43.484028°	173.12990°
Narbey Stream (T2)	-43.493845°	173. 24162°

All study streams were sampled on a single occasion over December-January during Summer 2016-2017. This time was selected as it overlaps with the maximum flight period of many caddisfly species (Smith et al. 2002). Streams were not sampled within three days of a rainfall event to allow species to recover from any possible flood. At each study stream I identified a 40 m reach, including a riffle and run complex where possible. I characterised reach-scale in-stream habitat by measuring wetted width, depth, and velocity at multiple points, following the protocol of Harding et al. (2009) (Table 11). A single water chemistry reading (i.e. pH, specific conductivity, and temperature) was collected at a single representative point using a YSI 63 meter (Table 11). Within each reach, I randomly selected 10 emergent cobble-boulders. These sized substrates are preferred egg-laying habitat for some stream insects (Reich & Downes 2003b, a; Storey et al. 2016). Several physico-chemical parameters were measured for each substrate (Table 10). These incorporated and built upon characteristics that have previously been shown to influence insect oviposition (Reich & Downes 2003a, b; Storey et al. 2016). Distance to the nearest bank was measured as the shortest distance between the vertical face of the substrate, and the stream bank. These measurements were divided by the wetted width to determine the proportionate lateral in-stream position of the substrate relative to stream size. Upstream depth and velocity were measured as close to the upstream face of the substrate as the necessary instruments would allow. Velocity was measured using a Flo-mate model 2000 portable flowmeter. Dissolved oxygen measurements were made at the upstream, downstream, and lateral faces of the substrate using a YSI Ecosense ODO 200 meter, and later averaged. The entire, and emergent portion of substrate was measured across three axes (length, width, and height). Total substrate surface area was later calculated as 1.15*(LW+LH+WH) (Graham et al. 1988); while the emergent portion surface area was calculated as LW+2LH+2WH, where L, W,

Table 10. Physico-chemical/habitat parameters measured at the microhabitat scale, and the expected fitness benefit/detriment for oviposited egg masses

Physico-chemical parameter	Oviposition cue
Distance to nearest bank (m)	Δ Disturbance refugia, proximity to stream access point
Distance to nearest bank/wetted width (%)	Δ Disturbance refugia, proximity to stream access point
Upstream depth (m)	Oviposition microhabitat availability, + desiccation refugia
Average dissolved oxygen (mg L^{-1})	+ Egg-mass survival
Average dissolved oxygen (%)	Δ egg mass survival
Upstream velocity (m s^{-1})	+ Shear, + larval drift
Total surface area (m^2)	+ Stability, + oviposition microhabitat availability
Emergent surface area (m^2)	+ Landing pad visibility, - oviposition microhabitat availability
Embeddedness (%)	- Oviposition microhabitat availability, + stability
Emergent moss cover (%)	- Oviposition microhabitat availability, + stability
Submerged moss cover (%)	- Oviposition microhabitat availability, + stability

and H correspond to length, width, and height axes of the measured substrate portion, respectively. Embeddedness was visually estimated as the percent of the total substrate surface area embedded in surrounding substrate. Similarly, emergent and submerged moss cover were visually estimated as a percentage of the emergent, and submerged, surface area of the substrate covered by moss, respectively. Egg masses were then photographed, identified and counted, and substrate was returned.

Habitat addition experiment

Okeover Stream was selected as the site for an experimental oviposition habitat addition. Okeover Stream is a small headwater tributary to the Avon River that runs through the University of Canterbury campus, Christchurch, New Zealand (Latitude -43.312306°, Longitude 172.351436°). Most of the water in Okeover Stream is aquifer sourced; however, is used to cool

several air conditioning systems around the school, before entering the stream. Albeit, water quality is generally good (Blakely & Harding 2005). This stream was subject to active riparian, channel, and in-stream habitat restoration between 1998–2005 (Winterbourn et al. 2007a). However, long reaches still have sparse emergent substrate. Correspondingly, taxa that require these substrate for oviposition are present, but rare (i.e. *Hydrobiosis parumbripennis*, *Austrosimulium sp.*, *Chironomus zealandicus*, and several cased caddisfly taxa) (Winterbourn 1978; Collier & Winterbourn 2000; Winterbourn et al. 2007a).

I collected 10 algae –free greywacke cobble-boulders from an inactive channel of the Waimakariri River, Christchurch and a further 10 algae-free igneous cobble-boulders from a small headwater stream in Banks Peninsula. The greywacke substrate had a characteristically smooth and rounded surface, while igneous substrate was comparatively rough and angular (Figure 10). All substrate was measured across three axes, allowing me to calculate an approximate surface area using the equation 1.15*(LW+LH+WH); where L, W, and H correspond to length, width, and height axes of the measured substrate portion, respectively (Graham et al. 1988). Substrate were then paired, so that each pair included a greywacke and igneous cobble-boulder with the most similar axial dimensions feasible (Figure 10).

True surface area measurements were then made for each cobble-boulder. This required each cobble-boulder to be wrapped in aluminium foil, which was then pressed into any irregularities on the substrate surface. Foil from each cobble-boulder was cut to only include that which was in contact with the substrate surface, then weighed. A 1 cm^2 aluminium foil cut-out was then weighed, and the weight of aluminium foil used to wrap each cobble-boulder was divided by the weight of the 1 cm^2 cut-out to provide an accurate description of substrate surface area. The surface area of rough surfaced substrate, when controlling for estimated size variation

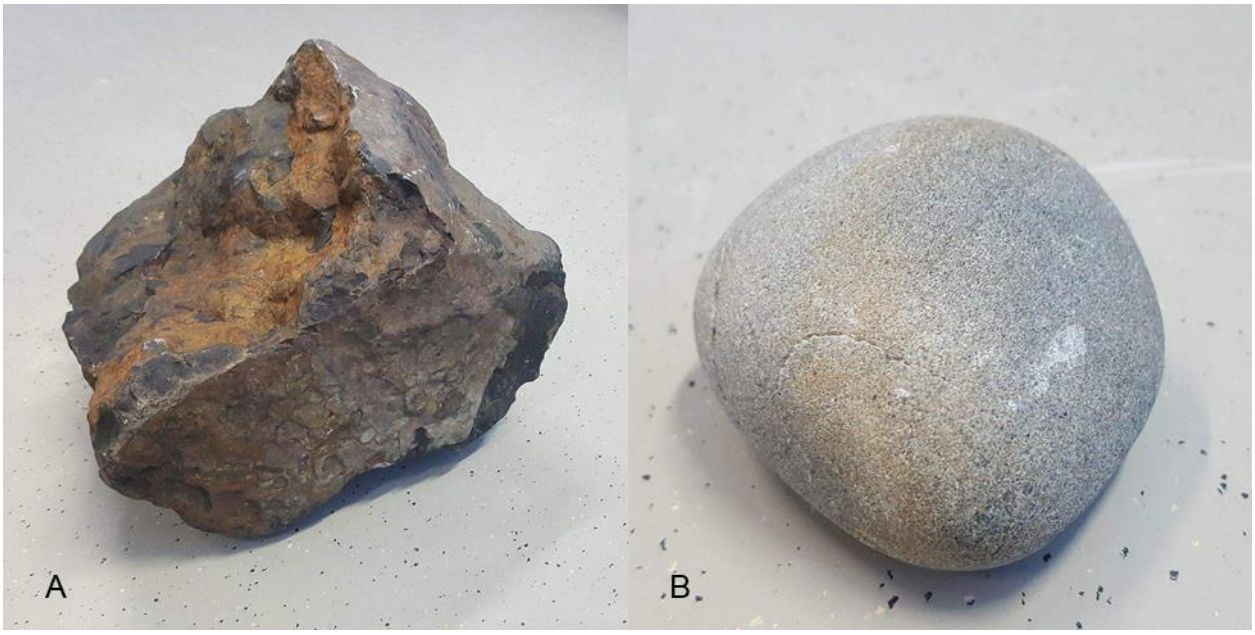

Figure 10. Representative substrate addition pairs used in Okeover Stream. A, rough-surfaced igneous substrate sourced from a Banks Peninsula headwater stream; and B, smooth-surfaced greywacke substrate sourced from the Waimakariri River. (Photo credit T. Green)

generated by axial measurements (i.e. 1.15*(LW+LH+WH)), was on average 11.9 (±8.5) % greater than smooth surfaced substrate.

On 28th November 2017, a 20 m reach was established in a run section of Okeover stream with homogenous in-stream habitat. Cobble-boulders were placed central to the channel in pairs, approximately 20 cm apart, perpendicular to the flow, in a random orientation. Subsequent substrate pairs were added longitudinally, separated by a 2 m gap.

Sampling was conducted on three occasions on one-week intervals following addition. On each occasion, substrate was removed from the stream, egg masses were identified by their morphological features (Figure 11C) and counted. Each cobble-boulder was then returned to the position in the stream from which it was removed.

Egg-mass identification

Most egg masses were identified on-site based on morphological features. Others were photographed and identified following personal communication with Brian Smith (NIWA) and Jon Harding (University of Canterbury). Family-level taxonomic classifications of all egg mass morphotypes were confirmed by a third-party (i.e. Jon Harding or Brian Smith) from photographs before proceeding to analysis.

Egg masses assigned to the Simuliidae family were observed in two morphotypes. One morphotype (Figure 11A) matched the morphological description of North Island *Austrosimulium australense* provided by Storey et al. (2016). These elongate, yellow-brown clusters measure 0.5–3 x 1–1.4 mm, are not laid in a defined order, and lack a clear gelatinous

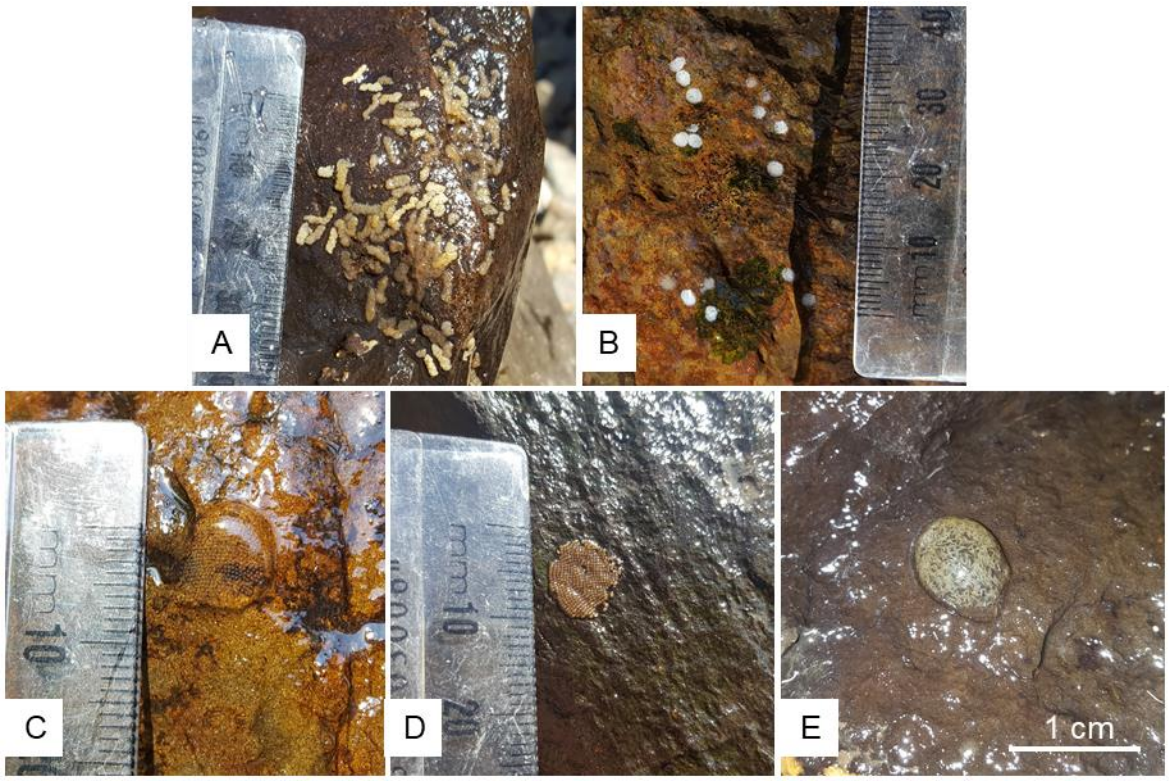

Figure 11. Insect egg masses on in-stream substrate in Banks Peninsula. A-B, similuliid egg masses with two distinct morphotypes; C, hydrobiosid egg mass; D, hydropsychid egg mass; E, unknown cased caddisfly egg mass. (Photo credit T. Green)

cover (spumaline) (Storey et al. 2016).The second morphotype (Figure 11B) has flat round discs of white eggs with a thin spumaline cover, measuring 1–2 x 1–2 mm. These characteristics were similar to those attributed to North Island *Austrosimulium sp.* egg masses by Storey et al. (2016).

Egg masses assigned to the Hydrobiosidae family were observed in a single distinctive morphotype (Figure 11C). These matched the morphological description of North Island hydrobiosid egg masses provided by Storey et al. (2016). They consist of a flat rounded disc with a spumaline cover, measuring 3–17 x 3–32 mm, and containing 100-1200 small white eggs in loosely packed rows (Storey et al. 2016).

Egg masses assigned to the Hydropsychidae family were morphologically similar to hydrobiosid egg masses yet varied in colour and lacked a spumaline cover (Figure 11D). They matched the morphological descriptions of North Island hydropsychid egg masses provided by Storey et al. (2016). Egg masses contain 80-750 red, brown or yellow eggs (depending on developmental stage), in tightly packed rows measuring 2–18 x 3–32 mm (Storey et al. 2016).

The egg masses depicted in Figure 11E were gelatinous and hemispherical–spherical in shape, containing small yellow–white eggs. The morphological characteristics and oviposition site of these egg masses were consistent with those of *Philorheithrus agilis* from the Southern Alps, as described by Winterbourn (1978). However, these characteristics also resembled those of conoesucid and *Hudsonemia* eggs observed in Waikato streams (Brian Smith, pers. comm.). Given the uncertainty regarding classification of these egg masses, they were more conservatively identified as a broader cased caddisfly group.

Data analysis

All data analysis was conducted using the open-source statistical data analysis software, R (R Core Team, 2013). For the field survey a binomial mixed effects model was used to test the

effect of substrate-scale physico-chemical/habitat parameters on the likelihood of the common hydrobiosid and simuliid, and combined taxa (i.e. including hydrobiosids, simuliids, cased caddisflies, and hydropsychids) ovipositing one or more egg masses on substrate, using the lme4 analysis package (Bates et al. 2014). Physico-chemical/habitat parameters were defined as fixed factors, while the stream was defined as a random factor to control for unexplained site-scale variation. Variance inflation factors (VIF) were identified. Physico-chemical/habitat parameters with VIF>5 were removed from the global model, reducing collinearity, and therefore correcting imprecisions in variance estimates, statistical significance, and ordinary least-squares estimators (Rogerson 2001; Jou et al. 2014). Stepwise AIC (Akaike information criterion) model selection was used to identify the most parsimonious model (i.e. a trade-off between the goodness of fit, and number of explanatory variables retained). This process involves the stepwise removal of insignificant predictor variables from a global model, while observing the resulting change in the AIC score. The most parsimonious model is defined when the removal of predictor variables no longer corresponds in a reduction in the AIC score (Symonds & Moussalli 2011).

A negative binomial mixed effects model was used to test the effect of substrate-scale physico-chemical/habitat parameters on the egg mass abundances of the common hydrobiosids and simuliids, and combined taxa, using the glmmADMB analysis package (Fournier et al. 2012). This model type was selected as the data set had greater variability than what was predicted from a Poisson model (overdispersion); the more conventional method for analysing count data. It follows the same mean structure as a Poisson regression, however adds an extra parameter to model overdispersion. Physico-chemical/habitat parameters were defined as fixed factors, while an observation-scale term nested within each study stream were defined as random factors to control for unexplained site-scale variation. For this analysis, I was only interested in

observations with ≥ 1 egg mass. This condition was imposed as the factors influencing the presence/absence of egg masses on substrate were assessed previously. The model was subject to VIF analysis, and stepwise AIC model selection to improve accuracy.

A Poisson mixed effects model was used to test the effect of substrate-scale physico-chemical/habitat parameters on the taxonomic richness of egg masses deposited on substrate, using the lme4 analysis package (Bates et al. 2014). Physico-chemical/habitat parameters were defined as fixed factors, while the study site was defined as a random factor to control for unexplained site-scale variation. For this analysis, I was only interested in observations with ≥ 1 egg masses, for abovementioned reasons. VIF analysis and stepwise AIC model selection were then used to define the most accurate model.

Pearson's correlation was used to test the extent of collinearity amongst the substrate-scale physico-chemical/habitat parameters. As logistic regression models are highly sensitive to correlation amongst predictor variables, conducting principal component analysis (PCA), and using principal components (PCs) in place of correlated physico-chemical/habitat parameters in this case allowed the incorporation of the full dataset, whilst not compromising the accuracy of model predictions (Tabachnick et al. 2001; Jou et al. 2014). PCA uses an orthogonal transformation to convert a set of potentially highly correlated variables into statistically independent PCs (McCreadie & Adler 1998). Each PC comprises a linear combination of correlated predictor variables expressed with varying degrees of influence (weights). PCA produces an equal number of PCs as original variables used; however, each subsequent PC explains a smaller portion of the variance from the original data set (i.e. PC1 explains the greatest portion of variance, followed by PC2). Correspondingly, eigenvalues and thus the interpretability of subsequent PCs decreases with number (Kaiser 1960). A scree plot was used

to determine an appropriate threshold for the number of PCs to be retained for further analysis. This was defined by a marked drop in the proportion of variance explained. Pearson's correlation was used to identify the extent that original physico-chemical/habitat parameters correlated with PCs and to define a correlation threshold (i.e. which original parameters significantly correlated with PCs). To reduce the risk of a Type 1 error and improve the interpretation of PCs, alpha levels were set at ≤0.001. The methods used to analyse the effects of PCs on egg mass presence/absence, abundance, and richness were almost synonymous to those used on the abovementioned original physico-chemical/habitat parameters. However, model selection through VIF and AIC methods was not required.

For the habitat addition experiment, 100% of egg masses identified on substrate belonged to a single free-living caddisfly family, Hydrobiosidae. Thus, it was not possible to test the effect of substrate surface complexity on egg mass richness. A negative binomial mixed effects model, from the glmmADMB package in R (Fournier et al. 2012; R Core Team, 2013), was used to test the hypothesis that ovipositing insects (hydrobiosids) will oviposit in greater abundances on complex surfaced substrate. Substrate surfaces were categorized as being either 'smooth', or 'rough', and defined as a fixed effect; while boulder pairs were nested within sampling occasion and defined as random effects.

Results

Field survey

Several reach-scale in-stream physico-chemical conditions were variable between survey sites, particularly specific conductivity, and mean water depth and velocity (Table 11). Although, all sites had a cobble dominated bed, near-neutral water pH, and low water temperature (Table 11).

Table 11. Reach-scale physico-chemical conditions for the eight streams surveyed on a single occasion in Summer 2016-2017. T1 = tributary one; T2 = tributary two

Site	pH	Specific Cond. (μS_{25} cm^{-1})	Temp. (°C)	Mean Vel. ($m\ s^{-1}$)	Mean Depth (m)	Mean Wetted Width (m)
Kaituna River	6.7	159	14.7	0.11	0.29	4.46
Okuti River	7.7	116	12.1	0.21	0.26	5.07
Pigeon Bay Stream	7.7	201	14.9	0.18	0.18	5.06
Wainui Bay Stream	7.6	83	12	0.19	0.12	2.95
Narbey stream	7.8	115	12.5	0.24	0.2	5.07
Narbey stream (T1)	8.1	71	10.8	0.23	0.16	1.01
Narbey stream (T2)	7.6	140	11.3	0.1	0.1	1.23
Balguerie Stream	7.5	117	9.9	0.17	0.15	3.33

In total, 1150 egg masses were observed across the 80 cobble-boulders sampled. The taxonomic groups depositing eggs included three families and one broader group. These included two caddisfly families of predatory-free living Hydrobiosidae, and net-spinning Hydropsychidae, the Diptera family Simuliidae, and cased caddisflies. In total, 69% of emergent substrate was used for oviposition. Amongst the observed taxa, hydrobiosids used 52.5% of substrate, simuliids 25%, cased caddisflies 12.5%, and hydropsychids 11.25% (Figure 12A). Simuliids were the most abundant taxa and oviposited on average 7.73 (±4.04 SE) egg masses per emergent cobble-boulder. These were closely followed by hydrobiosids (Mean 5.88 ± 1.35 SE), while cased caddisflies and hydropsychids were comparatively scarce, ovipositing on average 0.28 (±0.14) and 0.18 (±0.06) egg masses per emergent cobble-boulder, respectively (Figure 12B).

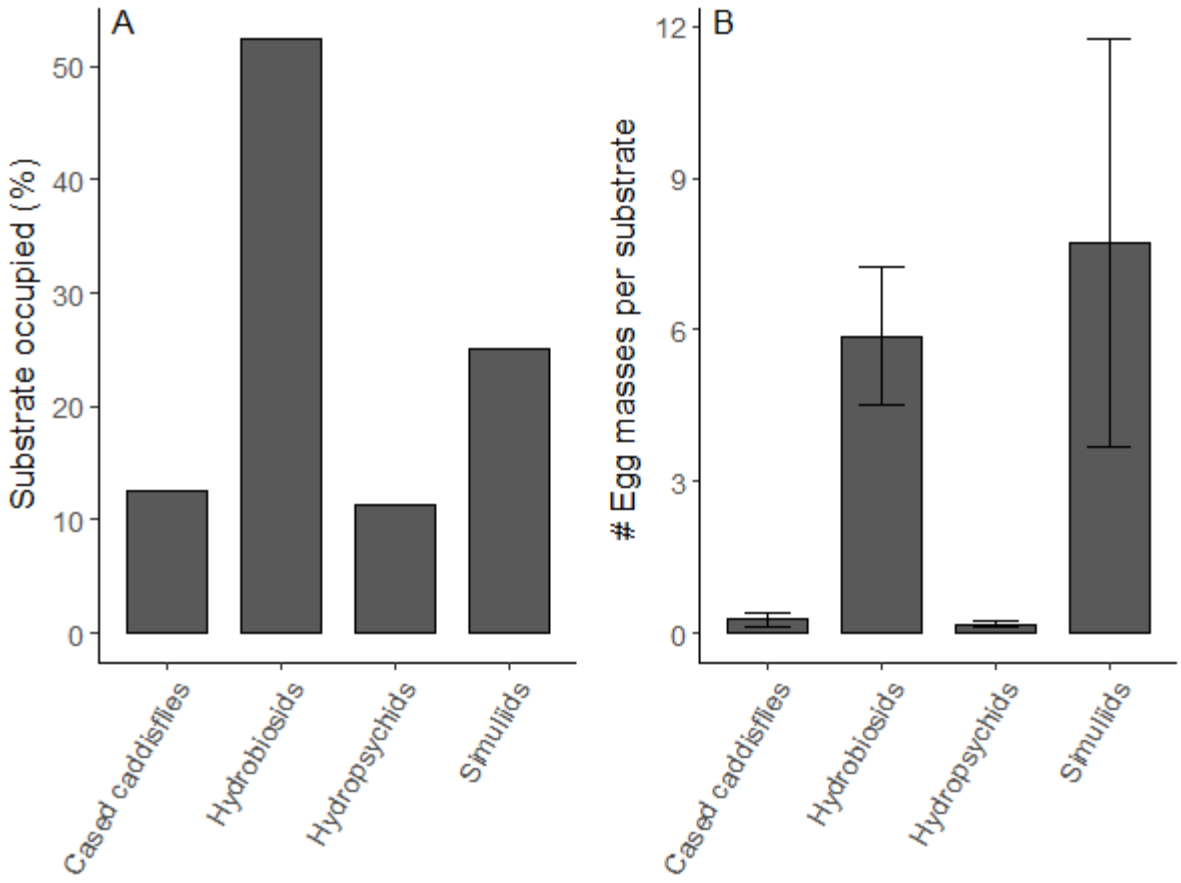

Figure 12. Emergent substrate use by ovipositing females amongst eight forested streams in Banks Peninsula. A, percent of surveyed substrates (n=80) occupied by egg masses from cased caddisflies, hydrobiosids, hydropsychids, and simuliids; and B, egg mass abundances ($\bar{x}$ ± SE) on emergent substrate amongst cased caddisfly, hydrobiosid, hydropsychid, and simuliid groups.

Factors influencing the presence/absence of egg masses

Hydrobiosid egg masses were significantly more likely to be present on substrate in faster flowing water with high dissolved oxygen saturation (%); however, less likely on embedded substrate (Table 12). Dissolved oxygen saturation had the greatest effect on the likelihood of one or more hydrobiosid egg masses being present, while the effects of velocity and embeddedness were of a similar lesser extent. Simuliid egg masses were significantly more likely to be present on substrate in water with higher dissolved oxygen saturation (Table 12). The degree of dissolved oxygen saturation surrounding substrate was an important cue for hydrobiosid and

simuliid oviposition. However, when egg masses from all taxa were pooled and analysed as a group, the extent of substrate embeddedness was the sole significant factor that negatively affected the likelihood of one or more egg masses being present (Table 12)

Table 12. Results from binomial mixed effects models, showing physico-chemical/habitat parameters influenced the presence/absence of egg masses deposited by hydrobiosid, simuliid, and combined (hydrobiosid, simuliid, cased caddisfly, and hydropsychid) taxa.

Taxa	Habitat	b	Std.error	z	p
Hydrobiosids					
	Dissolved oxygen (%)	16.797	6.685	2.513	**<0.05***
	Depth (m)	10.412	5.577	1.867	0.062
	Velocity (m s^{-1})	7.848	3.472	2.260	**<0.05***
	Emergent moss cover (%)	1.872	1.073	1.745	0.081
	Distance to bank (m)	1.296	0.813	1.594	0.111
	Embeddedness (%)	-6.990	3.481	-1.494	**<0.05***
	Dist.bank/wetted width (%)	-5.152	3.449	-1.494	0.135
Simuliids					
	Dissolved oxygen (%)	23.518	8.144	2.888	**<0.01****
	Dissolved oxygen (mg L^{-1})	-208.353	123.077	-1.693	0.090
	Depth (m)	-10.065	7.353	-1.369	0.171
	Dist.bank/wetted width (%)	-4.579	2.768	-1.643	0.100
	Shading (%)	-4.102	2.610	-1.572	0.116
	Emergent moss cover (%)	-2.680	1.998	-1.342	0.180
Combined taxa					
	Dissolved oxygen (%)	23.030	12.192	1.889	0.059
	Velocity (m s^{-1})	6.562	3.561	1.843	0.065
	Emergent cover (%)	2.049	1.399	1.465	1.430
	Dissolved oxygen (mg L^{-1})	-217.244	132.729	-1.637	0.102
	Shading (%)	-7.017	4.333	-1.619	0.105
	Embeddedness (%)	-5.244	2.337	-2.244	**<0.05***

Note: b = the slope/effect of physico-chemical/habitat parameters on the likelihood of an egg mass being present; Std. error = standard error; z = z-value; p = significance value (* = significant; ** = very significant; *** = highly significant).

Factors influencing egg mass abundance

Some parameters appeared to have strong effects on hydrobiosid and simuliid egg mass abundances independent of site-scale variability (i.e. dissolved oxygen and shading) (Figure 13), while other factors had more clear effects between substrate within sites (Table 13). Within sites,

Table 13. Results of negative binomial mixed effects models, showing physico-chemical/habitat parameters influenced the abundance of egg masses oviposited on substrate by hydrobiosid, simuliid, and combined (hydrobiosid, simuliid, cased caddisfly, and hydropsychid) taxa.

Taxa	Habitat	b	Std. error	z	p
Hydrobiosids					
	Embeddedness (%)	-6.235	2.135	-2.920	**<0.05***
	Shading (%)	-2.330	0.515	-4.520	**<0.001****
	Emergent moss cover (%)	-1.037	0.423	-2.450	**<0.05***
Simuliids					
	Dissolved oxygen (mg L^{-1})	659.581	134.970	4.890	**<0.001****
	Total surface area (m^2)	40.031	10.120	3.960	**<0.001****
	Emergent surface area (m^2)	-33.496	8.734	-3.840	**<0.001****
	Dissolved oxygen (%)	-27.362	7.528	-3.630	**<0.001****
	Depth (m)	-13.228	8.840	-1.500	0.135
	Embeddedness (%)	-9.973	3.401	-2.930	**<0.01****
	Emergent moss cover (%)	-2.487	1.277	-1.950	0.051
	Dist.bank/wetted width (%)	-0.072	0.020	-3.580	**<0.001****
Combined taxa					
	Dissolved oxygen (%)	9.696	2.922	3.320	**<0.001****
	Total surface area (m^2)	2.938	1.129	2.600	**<0.01****
	Shading (%)	-1.236	0.939	-1.320	0.188
	Emergent moss cover (%)	-1.167	0.508	-2.300	**<0.05***

Note: b = the slope/effect of physico-chemical/habitat parameters on egg mass abundance; Std. error = standard error; z = z-value; p = significance value (* = significant; ** = very significant; *** = highly significant).

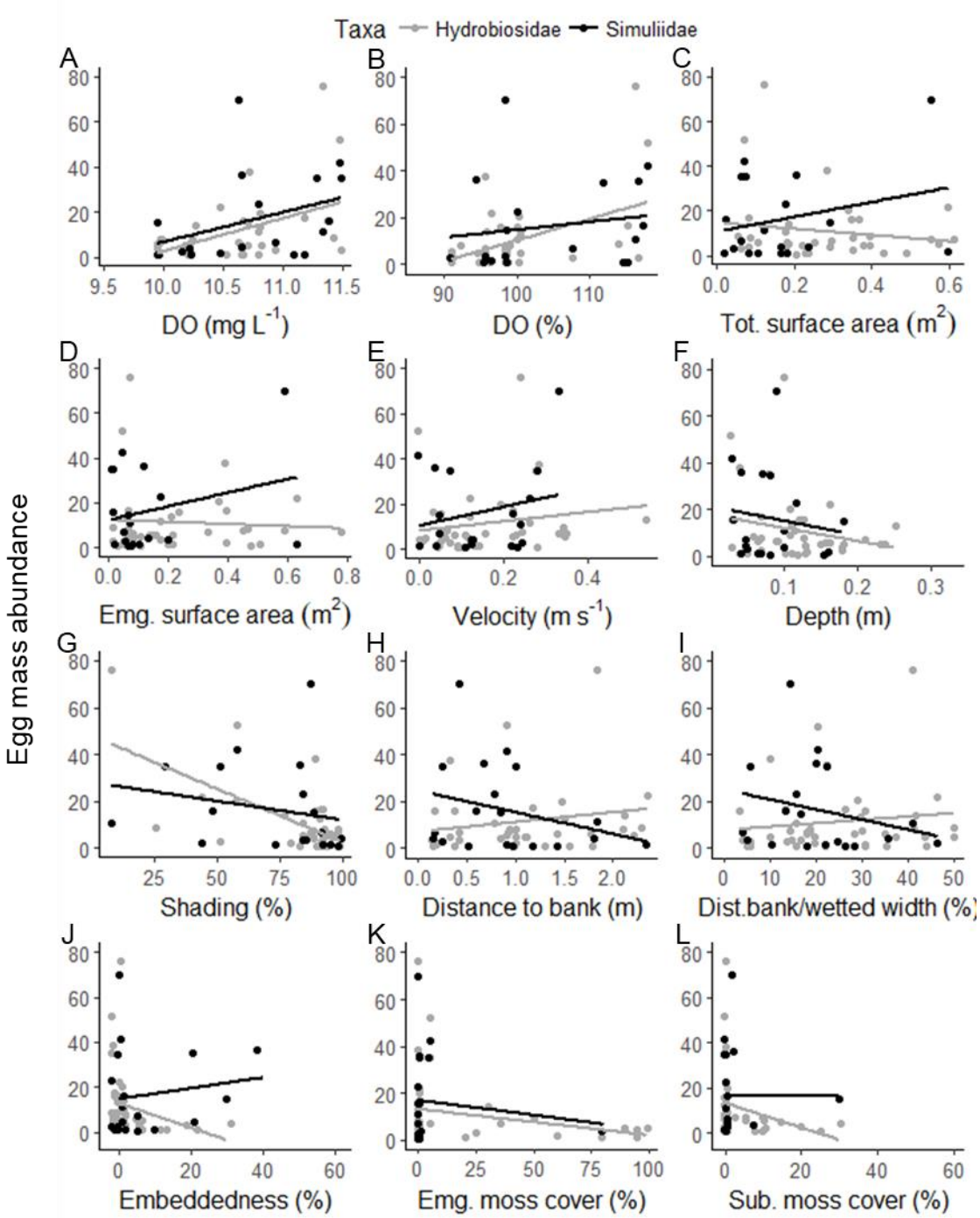

Figure 13. Egg mass abundances (≥1) of common hydrobiosid and simuliid taxa on emergent substrate across eight survey sites in Banks Peninsula, relative to physico-chemical/habitat parameters, including: A, dissolved oxygen (mg L^{-1}); B, dissolved oxygen (%); C, total surface area (m^2); D, emergent surface area (m^2); E, upstream velocity (m s^{-1}); F, upstream depth (m); G, shading (%); H, distance to bank (m); I, distance to bank/wetted width (%); J, embeddedness (%); K, emergent moss cover (%); L, submerged moss cover (%). Note: outlying data point (Simuliidae, n>300) removed to improve visual interpretation.

hydrobiosids oviposited significantly fewer egg masses on embedded, shaded, and emergent moss-covered substrate (Table 13). Substrate embeddedness had the greatest negative influence on hydrobiosid egg mass abundance, followed by shading and emergent moss cover. Simuliids oviposited significantly more on larger substrate, in water with higher dissolved oxygen concentrations (mg L^{-1}); however, significantly less on substrate that had large emergent portions, were highly embedded, distant from the bank, and in water with high dissolved oxygen saturation (%) (Table 13). The effect of dissolved oxygen concentration was an order of magnitude stronger than the next greatest effect size (total surface area). When egg masses from all taxa were pooled, higher egg mass abundances were significantly associated large substrate, in water with a high saturation of dissolved oxygen; while lower egg masse abundances were associated with extensive emergent moss cover (Table 13).

Factors influencing egg mass taxonomic richness

Of the 80 substrates sampled, 55 had egg masses from at least one insect family (or the broader cased caddisfly group), 23 had egg masses from two families, and two had egg masses from three families. As taxonomic groups were broadly defined (i.e. ≥ family level), and two of the four taxonomic groups assessed were rare, variance in taxonomic richness between substrate was limited. Considering these limitations there was no significant effect of physico-chemical/habitat parameters on taxonomic richness of egg masses.

Principal component analysis

Pearson's correlation showed that 33% of physico-chemical/habitat parameter pairs were significantly correlated (Table 14). Upon converting these parameters to principal components, PC 1 and 2 explained 44.5% of the variation in the data set, had eigen values >1, and preceded a

Table 14. Pearson's correlation table showing significantly correlated physico-chemical/habitat parameters ($p<0.05$).

Habitat parameter 1	Habitat parameter 2	Pearson's correlation	p
Total surface area	Emergent surface area	0.821	**<0.001*** **
Dissolved oxygen (%)	Dissolved oxygen (mg/L)	0.766	**<0.001*** **
Distance from bank	Distance from bank/wetted width	0.679	**<0.001*** **
Dissolved oxygen (%)	Shading	-0.595	**<0.001*** **
Shading	Dissolved oxygen (mg/L)	-0.533	**<0.001*** **
Depth	Total surface area	0.513	**<0.001*** **
Dissolved oxygen (%)	Total surface area	-0.386	**<0.001*** **
Distance from bank	Shading	-0.362	**<0.01** **
Emergent moss cover	Submerged moss cover	0.348	**<0.01** **
Total surface area	Dissolved oxygen (mg/L)	-0.328	**<0.01** **
Dissolved oxygen (%)	Emergent surface area	-0.319	**<0.01** **
Embeddedness	Submerged moss cover	0.296	**<0.01** **
Total surface area	Emergent moss cover	0.276	**<0.05***
Emergent surface area	Dissolved oxygen (mg/L)	-0.263	**<0.05***
Velocity	Embeddedness	-0.252	**<0.05***
Distance from bank	Depth	0.251	**<0.05***
Dissolved oxygen (%)	Distance from bank	0.235	**<0.05***
Distance from bank	Velocity	0.229	**<0.05***
Dissolved oxygen (%)	Velocity	0.228	**<0.05***
Shading	Velocity	-0.227	**<0.05***
Depth	Dissolved oxygen (mg/L)	-0.226	**<0.05***
Velocity	Emergent surface area	0.221	**<0.05***

steep drop in explained variance by subsequent PCs. PC1 and 2 were thus retained, and further analysis was based on these PCs.

PC1 explained 25.5% of the variation in the physico-chemical/habitat data. It was significantly positively correlated with measurements of total substrate surface area (69.5%), shading (65%), emergence (56.5%), emergent moss cover (38.4%), and upstream depth (36.5%); while significantly negatively correlating with dissolved oxygen saturation (%) (83.4%) and

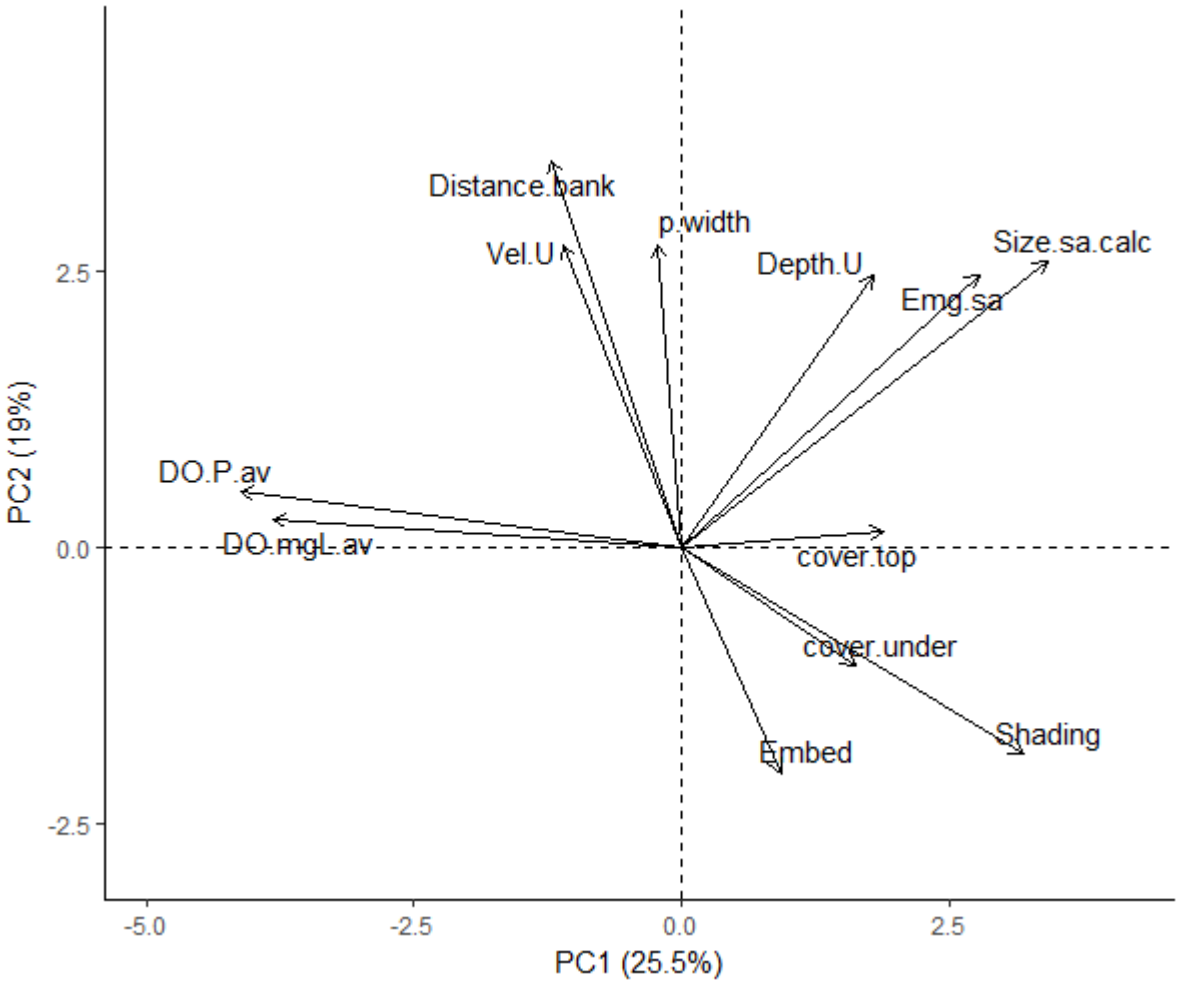

Figure 14. PCA biplot showing the influence of physico-chemical/habitat parameters on principal components one and two. The percentage of variability explained by each component is displayed on each axis. DO.mgL.av = mean dissolved oxygen concentration; DO.P.av = mean dissolved oxygen saturation; Vel.U = upstream velocity; Distance.bank, distance to the nearest bank; p.width = distance from bank/wetted width; Depth.U = upstream depth; Emg.sa = estimated surface area of the emergent substrate portion; Size.sa.calc = estimated total surface area of substrate; cover.top = emergent moss cover; cover.under = submerged moss cover; Embed = substrate embeddedness.

dissolved oxygen concentration (mg L^{-1}) (77.5%) (Figure 14). This suggests that these seven parameters vary together (i.e. larger substrates were often surrounded by water with lower dissolved oxygen saturation) (Table 14). PC1 is a measurement of these parameters relative to their respective weight (or correlation with the PC); thus, PC1 was foremost considered to represent in-stream dissolved oxygen. PC2 explained 19% of the variation. It was significantly positively correlated with measurements of distance from bank (71.3%), distance from

bank/wetted width (55.7%), upstream velocity (55.6%), total substrate surface area (52.7%), emergent surface area (50.3%), and upstream depth (50.1%); while significantly negatively correlating with embeddedness (41.3%), and shading (37.8%) (Figure 14). Thus, PC2 was foremost considered to represent distance from the bank.

For hydrobiosids, PC2 had a highly significant positive effect on the likelihood of one or more egg masses being oviposited on substrate (Table 15). Therefore, hydrobiosids were more likely to oviposit at greater distances from the stream bank, potentially influenced by the positively correlated effects of increased velocity, depth, and total and emergent substrate surface area; and the negatively correlated effects of embeddedness and shading. For simuliids, PC1 had a highly significant negative effect on the likelihood of one or more egg masses being oviposited on substrate (Table 15). Therefore, simuliids were more likely to oviposit on substrate in water with a high saturation and concentration of dissolved oxygen, potentially influenced by the

Table 15. Results from binomial mixed effects models, showing the effect of principal components one and two on the presence/absence of egg masses oviposited by hydrobiosid, simuliid, and combined (hydrobiosid, simuliid, cased caddisfly, and hydropsychid) taxa.

Taxa	PC	b	Std. error	z	p
Hydrobiosids					
	PC2	0.819	0.236	3.37	**<0.001*** **
	PC1	-0.309	0.213	-1.499	0.147
Simuliids					
	PC1	-0.722	0.201	-3.589	**<0.001*** **
	PC2	-0.128	0.211	-0.604	0.546
Combined taxa					
	PC2	0.796	0.2414	3.296	**<0.001*** **
	PC1	-0.31	0.214	-1.449	0.147

Note: PC = principal component; b = the slope/effect of PCs on the likelihood of an egg mass being present; Std. error = standard error; z = z-value; p = significance value (* = significant; ** = very significant; *** = highly significant).

negatively correlated effects of total and emergent substrate size, shading, emergent moss cover, and upstream depth. When egg masses from all taxa were pooled and analysed as a group, PC2 had a significant positive effect on the likelihood of one or more egg masses being oviposited on substrate (as with hydrobiosids).

The abundance of hydrobiosid egg masses on substrate was highly significantly negatively influenced by PC1, and very significantly positively influenced by PC2 (Table 16). Therefore, the results from PC1 suggest a greater number of hydrobiosids oviposited on substrate in water with higher saturation and concentration of dissolved oxygen, and potentially prefer smaller total and emergent substrate sizes, with little emergent moss cover and shading. While the results from PC2 suggest that greater numbers of hydrobiosids oviposit on substrate further from the bank, with greater velocity and depth, while embeddedness limited egg mass

Table 16. Results from negative binomial mixed effects models, showing the effect of principal components one and two on the abundance of egg masses oviposited by hydrobiosid, simuliid, and combined (hydrobiosid, simuliid, cased caddisfly, and hydropsychid) taxa.

Taxa	PC	b	Std. error	z	p
Hydrobiosids					
	PC1	-0.263	0.067	-3.940	**<0.001*** **
	PC2	0.258	0.096	2.700	**<0.01** **
Simuliids					
	PC1	-0.227	0.173	-1.313	0.190
	PC2	-0.087	0.232	-0.380	0.710
Combined taxa					
	PC1	-0.313	0.087	-3.580	**<0.001*** **
	PC2	0.157	0.117	1.330	0.182

Note: PC = principal component; b = the slope/effect of PCs on egg mass abundance; Std. error = standard error; z = z-value; p = significance value (* = significant; ** = very significant; *** = highly significant).

abundance. Neither PC1 or 2 significantly explained the variance in simuliid egg mass abundance across substrate (Table 16). However, when egg masses from all taxa were pooled and analysed as a group, PC1 had a significant negative effect on total egg mass abundance (as for hydrobiosids).

A Poisson mixed effects model found no significant effects of either PC1 or 2 on the taxonomic richness of egg masses oviposited on substrate.

Habitat addition experiment

Throughout the course of the experiment, all substrate additions were oviposited on by

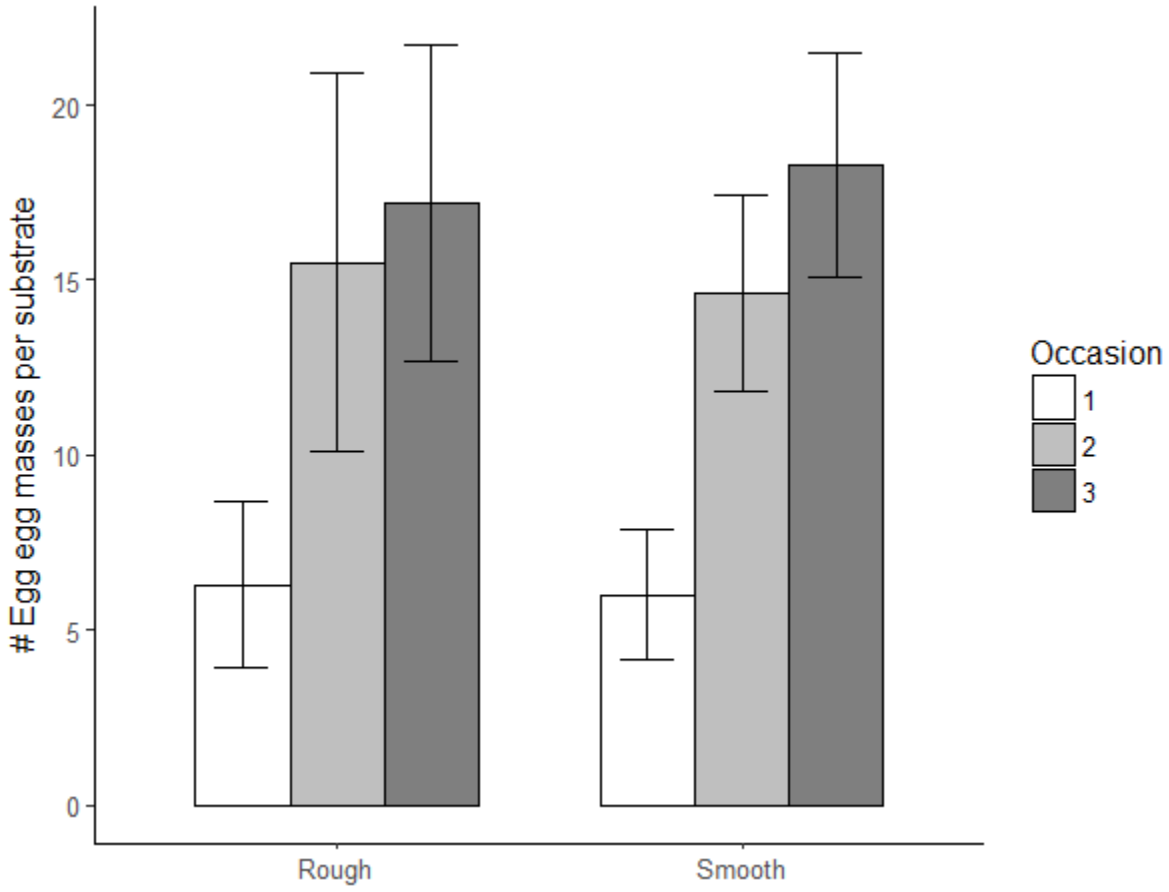

Figure 15. Hydrobiosid egg mass counts ($\bar{x}$ ± SE) on substrate pairs (n=20) with contrasting roughness (complexity) across three sampling periods.

hydrobiosid females. Egg mass counts on substrate increased over the three sampling occasions, indicative of continuous oviposition throughout the experiment. On the first sampling occasion, smooth surfaced substrate had received on average 6 (±1.86 SE) egg masses, while rough (complex) surfaced substrates had received 6.3 (±2.39 SE); on the second, smooth substrate had received on average 14.6 (±2.81 SE), while rough had received 15.5 (±5.41 SE); and on the third, smooth substrates had received on average 18.3 (±3.19 SE), while rough had received on average 17.2 (±4.53 SE) (Figure 15). However, a negative binomial mixed effects model found no significant difference in egg mass abundance between the two substrate surface complexity types ($b = 0.144$, $SE = 0.141$, $z = 1.02$, $p = 0.31$)

Discussion

Most freshwater restoration in New Zealand, and globally, focuses primarily on improving in-stream and/or bankside habitat. These often follow the much disputed assumption that improvements in local habitat heterogeneity will restore in-stream biodiversity (Palmer et al. 1997). However, recent reviews show that this approach is rarely successful (Palmer et al. 2010; Nilsson et al. 2015). I propose that part of this issue may result from the poorly understood constraints on insect dispersal. Several common New Zealand aquatic insect taxa seek out specific structural habitats to oviposit on (Winterbourn 1978; Collier & Winterbourn 2000). Additionally, evidence from the North Island and overseas shows that several of these families have preferences/limitations regarding the characteristics of substrate, and the immediately surrounding physico-chemical conditions (Reich & Downes 2003a, b; Bovill et al. 2013; Storey et al. 2016). Although, to what extent these factors might limit oviposition in lowland Canterbury waterways is currently unknown. This study aimed to identify the specific factors that promote and limit oviposition by aquatic insects in the Canterbury region. Identifying these factors will

enable practitioners to prioritise restoration activities relative to the dispersal and life-history modes of a regionally specific species pool.

It is likely that the taxonomic diversity of egg masses observed in this study was considerably higher than what is offered by my family level descriptions. However, due to a scarcity of research specifically describing the morphological characteristics of aquatic insect egg masses, more specific taxonomic identification (i.e. to genus or species level) was not feasible.

I surveyed insect oviposition habitat use in 8 forested Banks Peninsula streams, followed by a small-scale habitat addition experiment in an urban Christchurch stream to test the effect of substrate surface roughness on oviposition. It was evident that emergent substrate was an important oviposition habitat for some stream insects. Emergent substrate in Banks Peninsula streams received egg masses from the free-living caddisfly families Hydrobiosidae and Hydropsychidae, the dipteran Simuliidae, and a wider cased caddisfly group. Large emergent substrate situated in water with high dissolved oxygen saturation was preferred oviposition habitat by these combined taxa. However, moss cover and embeddedness appeared to have and inhibiting effect. These results were generally consistent with, and built upon, previous findings in New Zealand (Blakely et al. 2006; Storey et al. 2016), and Australia (Reich & Downes 2003a, b; Reich et al. 2011).

I found that hydrobiosid egg masses were more likely to be found on substrate in fast flows with high dissolved oxygen saturation. Higher velocity preferences are consistent with similar studies on Australian hydrobiosids (Reich & Downes 2003b, a; Bovill et al. 2013), and may indicate a higher tolerance to sheer stress relative to some Australian species (Bovill et al. 2013). Velocity did not affect hydrobiosid oviposition in a similar study conducted in Hamilton,

New Zealand (Storey et al. 2016), a noteworthy disparity indicative of the regional specificity of these findings. Dissolved oxygen availability was not a factor considered in other studies, however hydrobiosids had a strong preference for substrate with highly saturated surrounding water. There is no evidence to suggest adult caddisflies are adapted to detect small-scale variation in dissolved oxygen. However, visually turbulent surface water, which is associated with supersaturation (McKenna & McGillis 2004), has previously been shown to influence *Baetis* mayfly oviposition site selection in a North American study (Encalada & Peckarsky 2006). It is likely that this preference has associated egg mass fitness benefits from improved oxygen diffusion, such as reductions in developmental time (Loudon 1988; Greenberg & Ar 1996; Phillips & Moran 2015) and mortality (Morrison 1971). The converse relationships were found regarding substrate embeddedness and moss cover, and the extent of canopy cover. This latter finding was consistent with Storey et al. (2016), who also found this family to be most abundant in pasture streams. However, other studies have not considered the effect of moss cover, or measured embeddedness on a continuous scale (Blakely et al. 2006; Storey et al. 2016). As hydrobiosids oviposit on the substrate surface, usually on the underside (Reich & Downes 2003b, a; Storey et al. 2016), it is possible that emergent moss cover may be an indicator of poor exploitable surface availability on the submerged surface (i.e. if egg masses do not adhere to moss), while embeddedness directly limits the accessible submerged surface. These results build on those of Storey et al. (2016), who documented a marginal negative effect of categorical embeddedness. It is noteworthy, however, that while emergent moss cover and shading limited hydrobiosid egg mass abundances on substrate, only embeddedness was associated with an increased likelihood of zero-counts. The indifference for larger substrate by this family was suprising. Although consistent with a similar Australian study on hydrobiosid oviposition (Reich

& Downes 2003b). This finding contests that of Storey et al. (2016) in North Island streams. This disparity likely reflects one of two potential explanatory factors: (1) the size distribution of substrate in this survey was not sufficient to capture a statistically significant response; or, (2) substrate size does not influence oviposition site selectivity for this assemblage of hydrobiosids.

Like hydrobiosids, simuliids preferred to oviposit on unembedded substrate in highly saturated water. However curiously, DO saturation negatively affected simuliid egg mass abundance, while DO concentration had the opposite effect. It is possible that simuliids preferentially select substrate in water with high dissolved oxygen concentrations based on a visual cue (i.e. surface turbulence) (McKenna & McGillis 2004; Encalada & Peckarsky 2006); yet receive higher mortality due to sheer stress (i.e. Bovill et al. (2013)). However, this requires further investigation. Additionally, unlike hydrobiosids, substrate embeddedness did not increase the likelihood of zero-counts on substrate, however, abundances were reduced. This is likely the result of differentiation in microhabitat-scale oviposition site preferences, as simuliids do not primarily oviposit on the underside of substrate, the extent of microhabitat loss by embeddedness is less. Furthermore, greater abundances of simuliids oviposited on larger substrate, yet abundances reduced with substrate emergent portion size and distance from the bank. A preference for larger substrate is consistent with the findings of Storey et al. (2016), and could be attributed to the improved stability of these substrate (i.e. refuge from spates) (Matthaei et al. 1999).However, the inhibiting effect of substrate with large emergent portions contrasts the findings of Storey et al. (2016). Substrate with a large emergent areas inherently have decreased submerged surface area (i.e. the required oviposition habitat for these taxa). Thus, the egg mass carrying capacity of substrate may be limited. However, this relationship requires further investigation. Greater preferences for substrate closer to the bank is consistent with the patterns

observed by Storey et al. (2016). As New Zealand female simuliids have been reported to enter streams from the bank (Craig et al. 2012), these pattrerns may merely be an artifact of these insects locating emergent substrate closer to the stream bank first.

Principal component analysis provided insight into the intercorrelated nature of these lotic habitats, and the value of habitat heterogeneity for ovipositing insect communities. For example, the likelihood of hydrobiosid egg masses being present, as well as the abundance of egg masses on substrate, increased with PC2 (i.e. greater distance from the bank, reduced shading, higher water velocity and depth, and large unembedded substrate with large emergent portions). While the likelihood of simuliids being present, and the abundance of hydrobiosids, had the opposite relationship with PC1 (i.e. reduced dissolved oxygen, and increased substrate size, emergence, moss cover, shading, and water depth). These findings have potential implications for future stream management. For example, improving hydrobiosid oviposition may require large boulders to be placed centrally in restored reaches, where shading is reduced, flow is faster and deeper, and thus fine sediment accumulation is reduced. Similarly, improving oviposition by both taxa may first require remediation to in-stream dissolved oxygen concentrations.

Over the three-week period I conducted my substrate addition experiment, 100% of both rough and smooth surfaced substrate were used for oviposition by a single caddisfly family, Hydrobiosidae. It was therefore impossible to test the effect of substrate surface roughness on egg mass diversity. Hydrobiosids did not oviposit significantly more abundantly on rough-surfaced substrate. Egg mass abundances were surprisingly synchronous between the two substrate treatments across sampling occasions. It is likely that the small-scale preference for hydrobiosids to oviposit on the underside of substrate provides sufficient refugia from sheer

(Bovill et al. 2013; Storey et al. 2016). Thus, surface irregularities on rough-surfaced substrate may have been a redundant microhabitat for these taxa. However, whether substrate surface roughness can increase oviposition by other taxa remains unclear.

The shortcomings of my field experiment provided important insights into the efficacy of local oviposition habitat additions in lowland Canterbury. It was clear that my cobble-boulder additions provided sufficient oviposition habitat for hydrobiosids. However, no other taxa, including simuliids which share several oviposition habitat preferences with the hydrobiosids, oviposited on these substrates over a three-week period. As the adults of several larvae present in Okeover Stream use emergent substrate for oviposition (Collier & Winterbourn 2000; Winterbourn et al. 2007a), and this experiment was conducted during the expected peak flight period of many caddisflies and *Austrosimulium* (Smith et al. 2002; Craig et al. 2012), this depauperate oviposition may reflect the effects of reach-scale degradation. It is possible that local terrestrial habitat was not favoured by ovipositing adults (i.e. due to anthropogenic infrastructure, or limited vegetation density (Smith et al. 2002; Petersen et al. 2004; Blakely et al. 2006; Winterbourn et al. 2007b; Didham et al. 2012)), and larval populations were not reflective of local oviposition, but of downstream drift from more preferred habitat (Reich & Downes 2004).

Okeover stream is a headwater tributary, which has been subject to extensive in-stream and bankside restoration since c.1998, including the replanting of native flora in the riparian zone (Winterbourn et al. 2007a). This level of reach scale restoration is not common across Canterbury waterways. Lowland Canterbury has received extensive deforestation since early Polynesian settlement c.750 years ago, as well as intensive land-use practices across a land-scape scale. Consequentially, neither in-stream, or terrestrial habitats are sufficient to support many of

the taxa that are characteristic of the isolated forest fragments of Banks Peninsula. For example, Winterbourn et al. (2007b) found the adult distribution of several EPT taxa rarely extended beyond native forest habitats in South Island montane streams. Similarly, Didham et al. (2012) found that land-use change was the principal driver of adult aquatic insect community variation at a landscape scale in a similar South Island montane area. In addition, in-stream habitat degradation related to anthropogenic land-use change is frequently associated with degraded in-stream insect larval communities (Quinn & Hickey 1990; Quinn et al. 1992; Harding & Winterbourn 1995; Quinn et al. 1997; Hall et al. 2001). Consequentially, the dispersal of several forest specialist taxa to isolated sites with locally restored in-stream habitat is likely significantly constrained by a depauperate regional species pool in lowland Canterbury waterways.

My field survey of forested Banks Peninsula streams highlighted key factors characteristic of lowland Canterbury waterways that must be prioritised during restoration. For example, waterways are often inundated with fine sediment (embedded) with few large emergent substrates. However, my oviposition habitat addition experiment indicated that poor landscape connectivity may be the principal factor limiting adult aquatic insect dispersal to restored sites. Although, this inference was speculative, and further research with larger sample sizes is required. Likely fruitful pathways for future research may be to quantify the regional distribution of aquatic insects in both larval and adult life-stages. In doing so, source populations of taxa of conservation interest may be documented, and oviposition habitat restoration can be tailored relative to taxonomically specific dispersal ranges, and terrestrial and in-stream habitat requirements.

The results of this study provide several new insights into the oviposition habitat preferences of two stream invertebrate taxa that are common to waterways across Canterbury,

and New Zealand. The factors which were shown to consistently inhibit oviposition, such as substrate embeddedness, will be important considerations for future restoration projects in lowland Canterbury. My findings build upon similar research in the North Island and overseas and highlight a lack of generality for oviposition habitat preferences between regions. It was evident that several factors characteristic of lowland Canterbury waterways (i.e. depauperate large emergent structural in-stream habitat, and embeddedness from excess sedimentation) can limit insect oviposition. This will be an important consideration for the future of stream restoration in the region. However, the efficacy of localised restoration projects will likely be inhibited by landscape-scale degradation of both aquatic and terrestrial habitats in this region. Thus, I propose that future restoration need not prioritise the addition of habitat into isolated reaches, but focus on improving the connectivity between anthropogenically altered, and forested landscapes.

References

Bates D, Maechler M, Bolker B, Walker S 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1(7): 1-23.

Blakely TJ, Harding JS 2005. Longitudinal patterns in benthic communities in an urban stream under restoration. New Zealand journal of marine and freshwater research 39(1): 17-28.

Blakely TJ, Harding JS, Mcintosh AR, Winterbourn MJ 2006. Barriers to the recovery of aquatic insect communities in urban streams. Freshwater Biology 51(9): 1634-1645.

Bovill WD, Downes BJ, Lancaster J 2013. A test of the preference–performance hypothesis with stream insects: selective oviposition affects the hatching success of caddisfly eggs. Freshwater Biology 58(11): 2287-2298.

Collier K, Winterbourn M 2000. New zealand stream invertebrates: Ecology and implications for management. Hamilton, New Zealand, New Zealand Institute of Water and Atmosphere.

Craig DA, Craig RE, Crosby TK 2012. Simuliidae (Insecta: Diptera). Fauna of New Zealand 68.

Didham RK, Blakely TJ, Ewers RM, Hitchings TR, Ward JB, Winterbourn MJ 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundamental and Applied Limnology/Archiv für Hydrobiologie 180(1): 27-40.

Diehl S 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73(5): 1646-1661.

Encalada AC, Peckarsky BL 2006. Selective oviposition of the mayfly Baetis bicaudatus. Oecologia 148(3): 526-537.

Encalada AC, Peckarsky BL 2007. A comparative study of the costs of alternative mayfly oviposition behaviors. Behavioral Ecology and Sociobiology 61(9): 1437-1448.
Encalada AC, Peckarsky BL 2012. Large-scale manipulation of mayfly recruitment affects population size. Oecologia 168(4): 967-976.
Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27(2): 233-249.
Graham A, McCaughan D, McKee F 1988. Measurement of surface area of stones. Hydrobiologia 157(1): 85-87.
Greenberg S, Ar A 1996. Effects of chronic hypoxia, normoxia and hyperoxia on larval development in the beetle Tenebrio molitor. Journal of Insect Physiology 42(11-12): 991-996.
Hall MJ, Closs GP, Riley RH 2001. Relationships between land use and stream invertebrate community structure in a South Island, New Zealand, coastal stream catchment. New Zealand Journal of Marine and Freshwater Research 35(3): 591-603.
Hamilton A 1940. The New Zealand Dobson-fly (Archichauliodes diversus Walk.): Life-history and Bionomics. New Zealand Journal of Science and Technology 22(1A).
Harding J, Benfield E, Bolstad P, Helfman G, Jones E 1998. Stream biodiversity: the ghost of land use past. Proceedings of the national academy of sciences 95(25): 14843-14847.
Harding JS, Winterbourn MJ 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. New Zealand journal of marine and freshwater research 29(4): 479-492.
Harding JS, Clapcott JE, Quinn JM, Hayes JW, Joy MK, Storey RG, Greig HS, Hay J, James T, Beech MA and others 2009. Stream Habitat Assessment Protocols for wadeable rivers and streams in New Zealand, University of Canterbury, School of Biological Sciences.
Jaenike J 1978. On optimal oviposition behavior in phytophagous insects. Theoretical population biology 14(3): 350-356.
Jou Y-J, Huang C-CL, Cho H-J 2014. A VIF-based optimization model to alleviate collinearity problems in multiple linear regression. Computational Statistics 29(6): 1515-1541.
Kaiser HF 1960. The application of electronic computers to factor analysis. Educational and psychological measurement 20(1): 141-151.
Koivisto ME, Westerbom M 2010. Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores. Marine Biology 157(7): 1463-1474.
Lake P, Bond N, Reich P 2007. Linking ecological theory with stream restoration. Freshwater biology 52(4): 597-615.
Lancaster J, Downes BJ, Arnold A 2010. Environmental constraints on oviposition limit egg supply of a stream insect at multiple scales. Oecologia 163(2): 373-384.
Loudon C 1988. Development of Tenebrio molitor in low oxygen levels. Journal of Insect Physiology 34(2): 97-103.
Matthaei CD, Peacock KA, Townsend CR 1999. Patchy surface stone movement during disturbance in a New Zealand stream and its potential significance for the fauna. Limnology and Oceanography 44(4): 1091-1102.

Matthaei CD, Arbuckle CJ, Townsend CR 2000. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. Journal of the North American Benthological Society 19(1): 82-93.
McCreadie JW, Adler PH 1998. Scale, time, space, and predictability: species distributions of preimaginal black flies (Diptera: Simuliidae). Oecologia 114(1): 79-92.
McKenna S, McGillis W 2004. The role of free-surface turbulence and surfactants in air–water gas transfer. International Journal of Heat and Mass Transfer 47(3): 539-553.
Morrison G 1971. Dissolved oxygen requirements for embryonic and larval development of the hardshell clam, Mercenaria mercenaria. Journal of the Fisheries Board of Canada 28(3): 379-381.
Nilsson C, Polvi LE, Gardeström J, Hasselquist EM, Lind L, Sarneel JM 2015. Riparian and in-stream restoration of boreal streams and rivers: success or failure? Ecohydrology 8(5): 753-764.
Palmer MA, Ambrose RF, Poff NL 1997. Ecological theory and community restoration ecology. Restoration ecology 5(4): 291-300.
Palmer MA, Menninger HL, Bernhardt E 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 55: 205-222.
Parkyn SM, Smith BJ 2011. Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. Environmental management 48(3): 602-614.
Peckarsky BL, Taylor BW, Caudill CC 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. Oecologia 125(2): 186-200.
Petersen I, Masters Z, Hildrew A, Ormerod SJ 2004. Dispersal of adult aquatic insects in catchments of differing land use. Journal of Applied Ecology 41(5): 934-950.
Phillips NE, Moran AL 2015. Oxygen production from macrophytes decreases development time in benthic egg masses of a marine gastropod. Hydrobiologia 757(1): 251-259.
Poff NL 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the north american Benthological society: 391-409.
Quinn JM, Hickey CW 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. New Zealand journal of marine and freshwater research 24(3): 411-427.
Quinn JM, Williamson RB, Smith RK, Vickers ML 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 2. Benthic invertebrates. New Zealand journal of marine and freshwater research 26(2): 259-273.
Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand journal of marine and freshwater research 31(5): 579-597.
Reich P, Downes BJ 2003a. Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. Oecologia 136(3): 465-475.
Reich P, Downes BJ 2003b. The distribution of aquatic invertebrate egg masses in relation to physical characteristics of oviposition sites at two Victorian upland streams. Freshwater Biology 48(9): 1497-1513.
Reich P, Downes BJ 2004. Relating larval distributions to patterns of oviposition: evidence from lotic hydrobiosid caddisflies. Freshwater Biology 49(11): 1423-1436.

Reich P, Hale R, Downes BJ, Lancaster J 2011. Environmental cues or conspecific attraction as causes for egg mass aggregation in hydrobiosid caddisflies. Hydrobiologia 661(1): 351-362.
Rogerson P 2001. Statistical methods for geography, Sage.
Rowe RJ 1987. The dragonflies of New Zealand. The dragonflies of New Zealand.
Smith BJ, Collier KJ, Halliday NJ 2002. Composition and flight periodicity of adult caddisflies in New Zealand hill-country catchments of contrasting land use. New Zealand Journal of Marine and Freshwater Research 36(4): 863-878.
Storey R, Reid D, Smith B 2016. Oviposition site selectivity of some New Zealand aquatic macroinvertebrate taxa and implications for stream restoration. New Zealand Journal of Marine and Freshwater Research: 1-17.
Symonds MR, Moussalli A 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65(1): 13-21.
Tabachnick BG, Fidell LS, Osterlind SJ 2001. Using multivariate statistics.
Team RC 2013. R: A language and environment for statistical computing.
Thomaz SM, Dibble ED, Evangelista LR, Higuti J, Bini LM 2008. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. Freshwater biology 53(2): 358-367.
Winterbourn M 1978. The macroinvertebrate fauna of a New Zealand forest stream. New Zealand journal of zoology 5(1): 157-169.
Winterbourn MJ, Harding JS, McIntosh AR 2007a. Response of the benthic fauna of an urban stream during six years of restoration. New Zealand Natural Sciences 32: 1.
Winterbourn MJ, Chadderton WL, Entrekin SA, Tank JL, Harding JS 2007b. Distribution and dispersal of adult stream insects in a heterogeneous montane environment. Fundamental and Applied Limnology/Archiv für Hydrobiologie 168(2): 127-135.

Chapter 4 - Discussion

Freshwater ecosystems are fast approaching a state of crisis worldwide, driven primarily by the detrimental effects of habitat loss following the clear-cutting of native forests, and subsequent land-use practices (Collier 1993; Dudgeon et al. 2006). In response, stream restoration projects have greatly increased in popularity across developed nations, dominated both numerically and in total cost (>$500 million annually in the United States alone) by bankside and in-stream habitat manipulations (Bernhardt et al. 2005). Unfortunately, most of these projects receive little, if any pre and post-restoration monitoring, and recent findings indicate that those that do often do not meet restoration targets (Bernhardt et al. 2005; Bernhardt et al. 2007; Palmer et al. 2010). The failure of most stream restoration projects has been attributed to a disconnect between ecological theory and our knowledge of stream functioning, and restoration practice (Lake et al. 2007; Palmer et al. 2010).

Parkyn and Smith (2011) broadly identified three types of constraints which most limit full ecological recovery associated with stream restoration: dispersal, local habitat, and biotic constraints. These constraints interact and can be strongly influenced by landscape scale processes. Therefore, for restoration projects to be successful, they will need to specifically address all of these barriers. To date, a more holistic approach has not been applied systematically in the restoration of New Zealand's lowland waterways. The restoration of freshwater habitats in New Zealand has historically used the reestablishment and maintenance of riparian buffer zones a standard 'best practice' tool (McKergow et al. 2016). This practice has had positive effects on water quality by increasing shading (reducing water temperature) (Davies-Colley et al. 2009; Burrell et al. 2014), and mitigating diffuse pollution inputs (Smith

1987; Wilcock et al. 2013). However, the reestablishment of in-stream habitat heterogeneity/complexity through passive wood and leaf-litter additions is limited to the minority of projects that incorporated woody species in riparian plantings (Jones et al. 2016), and expected to take decades to centuries under current procedure (Meleason & Hall 2005; Davies-Colley et al. 2009). Additionally, expectations regarding the capacity of habitat additions to restore biodiversity, either following active additions or passively as riparian subsidies, are largely based on extrapolations from relationships observed in unimpaired river systems (Palmer et al. 2010; McKergow et al. 2016).

The effects of in-stream habitat on stream invertebrate communities

My study investigated whether in-stream habitat additions can restore benthic macroinvertebrate communities in lowland Canterbury waterways. Specifically, I focussed on two key constraints identified by Parkyn and Smith (2011); in-stream habitat and dispersal. This was addressed first by conducting a field survey of 11 forested South Island streams to identify whether benthic macroinvertebrate communities varied between habitat types (cobble-boulders, woody debris, leaf-packs, and gravel patches), and additionally to identify whether more abundant/diverse communities colonised habitat types that are atypical in channelised lowland Canterbury waterways (i.e. cobble-boulders, woody debris, and leaf-packs) (Chapter 2). I showed that benthic macroinvertebrate communities varied predictably amongst habitat types. My target habitats (i.e. cobble-boulders, woody debris, and leaf-packs) generally improved benthic macroinvertebrate assemblages based on several functional and compositional community metrics, relative to "controls" (i.e. gravel patches). These results were consistent with previous survey findings in forested New Zealand waterways (Jowett & Richardson 1990; Quinn & Hickey 1990; Jowett et al. 1991), and support previous propositions that microhabitat-scale

community compositions vary based on both requirements for stable habitat (Matthaei et al. 2000), and food resource partitioning (Collier & Halliday 2000). Gravel patches were an important incorporation in this survey, as they best represented the *status quo* bed habitat in many lowland Canterbury waterways. Thus, the addition of cobble-boulders, woody debris, and leaf-packs to lowland Canterbury waterways was expected to increase in-stream biodiversity by improving refugia and food subsidies. Subsequently, I conducted an experiment where I added cobble-boulders and wood blocks to three channelised lowland waterways to test whether these structures could improve in-stream benthic macroinvertebrate community compositions (Chapter 2). While these small-scale, short-term habitat additions promoted significantly more abundant benthic communities, they did not significantly improve compositional or functional diversity. Although this aspect of my study was novel for New Zealand waterways, it contests meta-analysis findings from intercontinental studies, which found these habitat additions improved taxonomic richness, but did not increase density/abundance (Miller et al. 2010). Limitations in monitoring time-periods, numbers of experimental sites, and numbers of habitat additions likely influenced my results however the failure of habitat additions to improve benthic community richness may be primarily attributed to poor landscape connectivity in the lowland Canterbury area. Results from this experiment indicate that larger substrate and wood availability may not be the primary factors limiting the recovery of macroinvertebrate communities in lowland Canterbury waterways, however they may provide improved flow refugia for some taxa.

Next, I conducted a survey of eight forested streams in Banks Peninsula, Canterbury, to identify whether adult aquatic insect dispersal may be constrained by preferred oviposition habitat availability (Chapter 3). I found that adult insects (primarily caddisflies and Simuliids) generally preferentially oviposited on large emergent substrate situated water with high dissolved

oxygen saturation, while selectively avoiding moss covered and embedded substrates. These results were generally consistent with previous findings in New Zealand (Blakely et al. 2006; Storey et al. 2016), and Australia (Reich & Downes 2003a, b; Reich et al. 2011). However, variation in family-level oviposition habitat preferences between my study and a similar study conducted in New Zealand's North Island (Storey et al. 2016), in conjunction with species level discrepancy between oviposition habitats documented overseas (Reich & Downes 2003a; Bovill et al. 2013), highlighted both the current limitations of aquatic insect egg mass taxonomic identification in New Zealand, and suggest discrepancies and knowledge gaps across regions. I also experimentally tested the hypothesis that more abundant and diverse assemblages of adult stream invertebrates would preferentially oviposit on complex emergent substrate (i.e. rough versus smooth-surfaced) (Chapter 3). My experiment showed that surface texture had no significant effect on egg mass abundance, and an inconclusive effect on richness. Part of the limitation of this study was that only a single family level group (Hydrobiosidae) oviposited on my substrate additions. These results indicated that preferred oviposition habitat availability may constrain aquatic insect dispersal in lowland Canterbury waterways (i.e. as they are characterised by high sediment cover, and thus embedded substrate). However, the highly limited species pool ovipositing on otherwise preferred substrate in my experimental stream indicated that greater-scale habitat degradation may be constraining adult insect dispersal.

Proposed limitations of local habitat restoration in lowland Canterbury

The restoration of aquatic macroinvertebrate community assemblages can be achieved by two often co-occurring pathways. First, through the enhancement of current in-stream populations; and second, through the dispersal and establishment of new taxa from a regional species pool. In lowland Canterbury, deforestation has occurred extensively since early Polynesian colonisation

c.750 years ago, and habitat degradation is prevalent (Ewers et al. 2006). Consequently, waterways are disconnected from forest habitats. As winged adults have a limited dispersal range, they are probably not able to physically reach many restored waterways (Smith et al. 2002; Petersen et al. 2004; Winterbourn 2005; Winterbourn et al. 2007). Also, adult aquatic insect dispersal is often influenced by the density and type of terrestrial vegetation cover, and several forested stream taxa have been found to preferentially avoid entering non-forested grasslands (Petersen et al. 2004; Winterbourn et al. 2007; Didham et al. 2012). Therefore, the likelihood of adult aquatic insects successfully dispersing from fragmented forests to isolated restoration sites in a land-scape otherwise dominated by anthropogenic land-use practices is unlikely. Furthermore, the widespread degradation of in-stream habitat (i.e. diffuse nutrient and sediment inputs, homogenised in-stream and bankside physical habitat (Williamson et al. 1992; Harding & Winterbourn 1995; Quinn et al. 1997; Harding et al. 1998)) can affect the success of dispersing adults and in-stream taxa at the landscape scale. The former was evident from my survey of oviposition habitat preferences in forested Banks Peninsula waterways (Chapter 3), where adult insects avoided ovipositing on microhabitat-scale features characteristic of impaired lowland waterways (i.e. smaller sized, embedded substrate) (Quinn et al. 1997; Burdon et al. 2013). Thus, I would expected that oviposition, and the subsequent recruitment of some taxa will be limited in lowland waterways with characteristically high deposited sediment cover (Blakely et al. 2006; Burdon et al. 2013). In-stream macroinvertebrate communities are often limited by habitat loss due to land-use practices, for example: the infilling of interstitial bed habitat with fine sediments (Burdon et al. 2013); nitrate associated toxicity (Camargo & Alonso 2006; Burdon et al. 2013) and eutrophication (Dodds & Welch 2000; McDowell et al. 2009); and, high water temperatures and wood/leaf litter depletion associated with historic riparian clearing

(Quinn et al. 1997). These waterways often generate poor in-stream macroinvertebrate habitat which results in simplified macroinvertebrate communities. Thus, the regional species pool for lowland Canterbury waterways is largely limited to tolerant taxa. The wider degradation of these waterways poses a major limitation to the efficacy of localised restoration approaches, as in this study, as the pathway to restoration is limited to enhancing the populations of taxa that are already present in the waterway or encouraging the dispersal of taxa from nearby waterways with likely similarly depauperate fauna. These limitations were evident from both experimental phases in my study. For example, oviposition habitat additions in a single urban waterway in Christchurch (Chapter 3) received egg masses from a single insect group, the intermediately tolerant, in-stream and terrestrial habitat generalist, Hydrobiosidae (Jowett et al. 1991; Smith et al. 2002; Stark & Maxted 2007); and while in-stream cobble-boulder and wood additions improved macroinvertebrate abundances in my study streams, they did not correspond to an increase in taxonomic richness (Chapter 2). Notably, this subset of in-stream physical habitat was limited in their capacity to improve microhabitat-scale macroinvertebrate community richness across several compositional and functional metrics, when surveyed in forested Banks Peninsula streams (Chapter 2).

Future directions in New Zealand freshwater restoration

This thesis addressed how in-stream structural habitat additions can alleviate two major factors that limit stream restoration, dispersal and local habitat constraints (Parkyn & Smith 2011). However, given the limitations posed by this study and research in this field, further investigation on this topic is warranted. Future aquatic restoration in New Zealand must consider these extensive limitations when setting restoration goals, especially in the short term. In the long term, it is essential that future research directs restoration practitioners towards re-establishing

the connectivity between forested, and adjacent anthropogenically altered landscapes. In the case of restoring the connectivity between healthy and degraded aquatic macroinvertebrate community assemblages, special consideration must be made towards the complex life-histories of these fauna (i.e. taxonomically specific dispersal limitations, and habitat requirements at both terrestrial and aquatic life-stages (Jowett et al. 1991; Petersen et al. 2004; Winterbourn 2005; Winterbourn et al. 2007; Didham et al. 2012)). This may be achieved by prioritising restoration activities in close proximity to source populations, for example, previous studies have indicated a dramatic reduction in restoration lag-time when restoration sites were situated adjacent to source populations of target species (Huxel & Hastings 1999). Also, the establishment of forested dispersal corridors, potentially through the enhancement of riparian buffer zones, can have positive effects on land-scape connectivity of terrestrial insects (Öckinger & Smith 2008). Given the known land-use associated dispersal limitations of several adult aquatic insect taxa (Smith et al. 2002; Winterbourn 2005; Winterbourn et al. 2007; Didham et al. 2012), corridors connecting forested waterways with nearby waterways of contrasting land-uses may be a logical step towards remediating dispersal constraints, and potentially restoring regional species pools. However, given a lack of empirical research surrounding these tools in a New Zealand context, insights from thesis into their efficacy remain preliminary. Notwithstanding, restoration in New Zealand would be significantly more effective with the adoption of large-scale adaptive management, in conjunction with the incorporation of previously established limitations on ecosystem recovery (Schreiber et al. 2004). Identifying and addressing the factors which most limit restoration, on a case-by-case basis, and effectively ‘ruling out’ limitations from the landscape, to the scale of local microhabitat and biotic interactions is needed (Poff 1997; Palmer et al. 2010). Logical early steps in this process for lowland Canterbury waterways would be the

reestablishment of adult dispersal connectivity, as indicated by the wide-scale degradation of forested habitat and stream biota, and more specifically by the limited efficacy of my habitat additions to restore biodiversity in these waterways. Subsequently, with the alleviation of larger scale degradation, the efficacy of local habitat manipulations can be more accurately assessed. Future studies will likely benefit by restoring local habitat to reference conditions (i.e. by restoring riparian zones, channel morphology, and in-stream structural habitats to some pre-degraded state) at headwater sites, and extensively monitoring the reach-scale effects over several years, or decades (see Harding et al. (1998)).

Conclusion

In-stream habitat clearly performs an important role in the spatial distribution, and recruitment of benthic macroinvertebrates in forested streams. However, the reestablishment of in-stream habitat currently has limited efficacy as a restoration tool in lowland Canterbury waterways. I attributed this disconnect to larger-scale habitat degradation, and the fragmentation and isolation of these waterways from source populations in forested waterways. This thesis provides a valuable contribution to New Zealand freshwater restoration literature and the first known test of habitat addition/manipulations and habitat suitability survey for lowland Canterbury. Previously, it was unclear whether the lowland Canterbury landscape would facilitate or inhibit stream restoration using simple inexpensive habitat additions. It is now clear that although in-stream habitat performs an important role in stream invertebrate communities in forested South Island waterways, the restoration of aquatic invertebrate communities in lowland Canterbury waterways requires that the remediation of larger-scale habitat degradation is prioritised, before local habitat additions are likely to be an effective tool.

References

Bernhardt ES, Palmer MA, Allan J, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J 2005. Synthesizing US river restoration efforts. Science 308(5722): 636-637.

Bernhardt ES, Sudduth EB, Palmer MA, Allan JD, Meyer JL, Alexander G, Follastad-Shah J, Hassett B, Jenkinson R, Lave R 2007. Restoring rivers one reach at a time: results from a survey of US river restoration practitioners. Restoration Ecology 15(3): 482-493.

Blakely TJ, Harding JS, Mcintosh AR, Winterbourn MJ 2006. Barriers to the recovery of aquatic insect communities in urban streams. Freshwater Biology 51(9): 1634-1645.

Bovill WD, Downes BJ, Lancaster J 2013. A test of the preference–performance hypothesis with stream insects: selective oviposition affects the hatching success of caddisfly eggs. Freshwater Biology 58(11): 2287-2298.

Burdon FJ, McIntosh AR, Harding JS 2013. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. Ecological Applications 23(5): 1036-1047.

Burrell TK, O'Brien JM, Graham SE, Simon KS, Harding JS, McIntosh AR 2014. Riparian shading mitigates stream eutrophication in agricultural catchments. Freshwater Science 33(1): 73-84.

Camargo JA, Alonso Á 2006. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: a global assessment. Environment international 32(6): 831-849.

Collier K 1993. Review of the status, distribution, and conservation of freshwater invertebrates in New Zealand. New Zealand journal of marine and freshwater research 27(3): 339-356.

Collier KJ, Halliday JN 2000. Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: stable habitat or trophic subsidy? Journal of the North American Benthological Society 19(1): 94-111.

Davies-Colley RJ, Meleason MA, Hall RM, Rutherford JC 2009. Modelling the time course of shade, temperature, and wood recovery in streams with riparian forest restoration. New Zealand Journal of Marine and Freshwater Research 43(3): 673-688.

Didham RK, Blakely TJ, Ewers RM, Hitchings TR, Ward JB, Winterbourn MJ 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundamental and Applied Limnology/Archiv für Hydrobiologie 180(1): 27-40.

Dodds WK, Welch EB 2000. Establishing nutrient criteria in streams. Journal of the North American Benthological Society 19(1): 186-196.

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A-H, Soto D, Stiassny ML 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological reviews 81(2): 163-182.

Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK 2006. Past and future trajectories of forest loss in New Zealand. Biological Conservation 133(3): 312-325.

Harding J, Benfield E, Bolstad P, Helfman G, Jones E 1998. Stream biodiversity: the ghost of land use past. Proceedings of the national academy of sciences 95(25): 14843-14847.

Harding JS, Winterbourn MJ 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. New Zealand journal of marine and freshwater research 29(4): 479-492.

Huxel GR, Hastings A 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7(3): 309-315.
Jowett IG, Richardson J 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for Deleatidium spp. New Zealand journal of marine and freshwater research 24(1): 19-30.
Jowett IG, Richardson J, Biggs BJ, Hickey CW, Quinn JM 1991. Microhabitat preferences of benthic invertebrates and the development of generalised Deleatidium spp. habitat suitability curves, applied to four New Zealand rivers. New Zealand journal of marine and freshwater research 25(2): 187-199.
Lake P, Bond N, Reich P 2007. Linking ecological theory with stream restoration. Freshwater biology 52(4): 597-615.
Matthaei CD, Arbuckle CJ, Townsend CR 2000. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. Journal of the North American Benthological Society 19(1): 82-93.
McDowell R, Larned S, Houlbrooke D 2009. Nitrogen and phosphorus in New Zealand streams and rivers: control and impact of eutrophication and the influence of land management. New Zealand Journal of Marine and Freshwater Research 43(4): 985-995.
McKergow LA, Matheson FE, Quinn JM 2016. Riparian management: A restoration tool for New Zealand streams. Ecological Management & Restoration 17(3): 218-227.
Meleason MA, Hall GM 2005. Managing plantation forests to provide short-to long-term supplies of wood to streams: a simulation study using New Zealand's pine plantations. Environmental Management 36(2): 258-271.
Miller SW, Budy P, Schmidt JC 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. Restoration Ecology 18(1): 8-19.
Öckinger E, Smith HG 2008. Do corridors promote dispersal in grassland butterflies and other insects? Landscape Ecology 23(1): 27-40.
Palmer MA, Menninger HL, Bernhardt E 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 55: 205-222.
Parkyn SM, Smith BJ 2011. Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. Environmental management 48(3): 602-614.
Petersen I, Masters Z, Hildrew A, Ormerod SJ 2004. Dispersal of adult aquatic insects in catchments of differing land use. Journal of Applied Ecology 41(5): 934-950.
Poff NL 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the north american Benthological society: 391-409.
Quinn JM, Hickey CW 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. New Zealand journal of marine and freshwater research 24(3): 411-427.
Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand journal of marine and freshwater research 31(5): 579-597.
Reich P, Downes BJ 2003a. Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. Oecologia 136(3): 465-475.

Reich P, Downes BJ 2003b. The distribution of aquatic invertebrate egg masses in relation to physical characteristics of oviposition sites at two Victorian upland streams. Freshwater Biology 48(9): 1497-1513.
Reich P, Hale R, Downes BJ, Lancaster J 2011. Environmental cues or conspecific attraction as causes for egg mass aggregation in hydrobiosid caddisflies. Hydrobiologia 661(1): 351-362.
Schreiber ESG, Bearlin AR, Nicol SJ, Todd CR 2004. Adaptive management: a synthesis of current understanding and effective application. Ecological Management & Restoration 5(3): 177-182.
Smith BJ, Collier KJ, Halliday NJ 2002. Composition and flight periodicity of adult caddisflies in New Zealand hill-country catchments of contrasting land use. New Zealand Journal of Marine and Freshwater Research 36(4): 863-878.
Smith CM 1987. Sediment, phosphorus, and nitrogen in channelised surface run-off from a New Zealand pastoral catchment. New Zealand journal of marine and freshwater research 21(4): 627-639.
Stark J, Maxted JR 2007. A user guide for the Macroinvertebrate Community Index. Prepared for the Ministry for the Environment: 58.
Storey R, Reid D, Smith B 2016. Oviposition site selectivity of some New Zealand aquatic macroinvertebrate taxa and implications for stream restoration. New Zealand Journal of Marine and Freshwater Research: 1-17.
Wilcock R, Monaghan R, Quinn J, Srinivasan M, Duncan M, Scarsbrook M 2013. Trends in water quality of five dairy farming streams in responses to changes in farm management and adoption of best practice: benefits of long-term monitoring at the catchment scale. Mar Freshw Res 64: 401-412.
Williamson RB, Smith RK, Quinn JM 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 1. Channel form and stability. New Zealand journal of marine and freshwater research 26(2): 241-258.
Winterbourn MJ 2005. Dispersal, feeding and parasitism of adult stoneflies (Plecoptera) at a New Zealand forest stream. Aquatic Insects 27(3): 155-166.
Winterbourn MJ, Chadderton WL, Entrekin SA, Tank JL, Harding JS 2007. Distribution and dispersal of adult stream insects in a heterogeneous montane environment. Fundamental and Applied Limnology/Archiv für Hydrobiologie 168(2): 127-135.